THE OPEN UNIVERSITY
A SCIENCE FOUNDATION COURSE

UNIT 19 LIFE AND EVOLUTION

THE SCIENCE FOUNDATION COURSE TEAM

The illustration on the front cover shows the typical form of the peppered moth, *Biston betularia*, resting and visible on a dark tree trunk.

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1.2

BIOLOGY

STUDY GUIDE

This Unit is the first of the biology Units in S102. It has two components only, the text and a television programme. Sections 1 and 2 introduce you to a number of important biological ideas, setting the scene for topics that are introduced systematically and in some detail later on in this and the succeeding Units. One of the ideas introduced in these Sections is that of evolution—and this is the theme of Sections 3–7. The story of evolution, after exploring the nature of inheritance in Unit 20, continues in Unit 21.

The style of much of this Unit is different from that of several of the preceding ones in the Course. Some areas of biology, including those covered in this Unit, need extended discussion. Parts of the Unit, notably Sections 3–7, are discursive in character. They do not contain long lists of hard facts that have to be memorized, but do contain careful assessments of specific bodies of evidence. Some people find this approach 'waffly' and unsatisfying. But assessment of evidence and argument in support of or against a particular theory is a vital part of science, and you should use this Unit to become familiar with this important aspect of it.

The TV programme, beginning in Darwin's study at Down House in Kent, compares the almost overwhelming diversity of life with the striking underlying unity of cellular and chemical patterns. The programme can be watched at any time during your study of this Unit—though you would make more of the programme if you have read most of the Unit before seeing it.

Later on in your study of the Biology Units (Unit 25) there is an Experiment which requires you to collect 40 leaves from a holly bush. Holly is quite common in most parts of Britain, but we strongly recommend that you check *now* that you can locate a bush. If you live in an area where holly can't be found easily, you should seek help from your study centre (tutor or tutor-counsellor) so that special arrangements can be made well in advance of your study of Unit 25. Leaves can be collected and then stored for 6 weeks or more in a refrigerator. You could collect your sample at any time from now on, but check the details in Unit 25, Section 4.4 first, because only leaves with certain features are required.

INTRODUCTION: BIOLOGY

Biology is the study of life: the word means exactly that—*bios* is Greek for life and *logos* is Greek for word or study. This Unit is the first of eight biology Units and you will start with your own views of what the subject may be about, and whether it will turn out to be easy or difficult, boring or pleasing.

Some years ago biology was very recognizably about whole animals and plants. Students dissected dogfish and examined flowers. Some categorized it as a descriptive and non-numerical subject, almost a soft option. In recent times, in contrast, biological knowledge on all fronts has been increasing with awesome rapidity, driven partly at least by society's recognition of the capacity of modern biology to influence the way humans live their lives. The disease of AIDS, caused by a virus, will, if unchecked, cull our own population in the 1990s as surely as the Black Death bacterium halved Britain's population in the 14th century. But, whether through induced changes in human behaviour (by means of subtle psychological techniques underlying advertising), or through advances in molecular biology which will allow us to combat this virus, or through increases in our knowledge of immunity, it is clear that biology offers a major hope of relief.

ORGANS

TISSUES

CELLS

Equally dramatic, and arguably more important, is the question of growing sufficient food for a burgeoning world population. Solving this problem without promoting still further growth of the population, and without destroying the environment in which the food is grown will require the help of many branches of biology. There is an apparently endless list of other, less apocalyptic examples of the relevance of biology to our everyday lives: it is crucially and commercially involved in the manufacture of chemicals, fuels, and pharmaceuticals, in the development of medicine and agriculture, and in specialist industries such as brewing and food processing. Biology is profoundly important in everyday life, and you will find many examples in these Units demonstrating this very point. But there is more to biology than this. The subject matter of biology, life itself, is astonishingly beautiful and diverse, and we hope that you will come to appreciate this beauty and diversity more fully as you study the Units. Lastly, biology contains some of the great ideas of science: Darwin's theory of natural selection, Mendel's theory of inheritance, the concept of the genetic code, to mention only three. To understand these ideas is to come that bit closer to understanding the mysteries of life. And this, in Section 2, is where we begin: what do we mean by 'life'?

2 WHAT IS LIFE?

There is no short or crisp answer. Indeed, for a phenomenon that has been around on this planet for about 4 000 million years, that is so conspicuously present in almost every corner of it, and that encompasses creatures of such intellectual vanity as ourselves, it would be disappointing if there were an easy answer! There are, however, various major features of life that we look briefly into in this Section, and explore more fully later—in this and other Units.

2.1 THE DIVERSITY OF LIFE

What images spring to mind when you hear the phrase 'The living world'? Many people think of elephants, zebras, lions and other big game sweeping across the plains of Africa, of humming-birds sucking nectar from flamboyant tropical flowers, of humid tropical forests, or of shoals of fish browsing among coral reefs. Thanks to the superb natural history programmes that appear on television nowadays, it is possible to get an idea of the rich variety of animal and plant life. But even with the help of these programmes it is difficult to grasp the full scale of life. In the animal world alone, there are well over a million different kinds (the technical word is species) of organism. About three-quarters of a million of these are insects and about 290 000 of these species of insects are beetles. So, if you were asked to name a typical animal, perhaps your answer should be a beetle. But perhaps it should not, for if you were to look for the kind of animal that was more numerous in terms of individual bodies than any other on Earth, you should probably choose a kind of worm, belonging to a group of animals called the nematodes. These live in the soil, the sea, in fresh water and as parasites, and most are less than 1 mm long. The sheer numbers of these animals in the world prompted the author of a well-known textbook on animals once to observe that if our entire planet and all of its living occupants except for these worms were to become invisible, the Earth would still be clearly visible from space as a hollow sphere, consisting of nothing but nematodes.

It is not simply the numbers of animals and plants that are so extraordinary, it is their way of life. In Britain we are so used to the seasons and to the annual flowering of plants that it comes as a surprise to find that some bamboos in Asia flower only once, after a period of 90 years, and then die. We are so familiar with the fact that insects are attracted to flowers, are rewarded with nectar, and in drinking the nectar help to pollinate the

flowers, that we find it bizarre that some plants use other ways of luring insects to them to achieve pollination. The flowers of the orchid *Ophrys insectifera*, for example, bear an extraordinary similarity to a certain kind of female wasp. So good is the resemblance that male wasps belonging to that species try to mate with the flowers, and in so doing help to pollinate the plant. Among the animals, we find it easiest to identify with those that are built most like ourselves and have ways of life that have at least some parallels with our own. Chimpanzees are one obvious example, with the elaborate care they lavish on their infants, and, sadly, with their own form of warfare. But what about termites, bees and other insects that live in colonies of thousands? A queen termite is nothing but an egg-laying machine, producing up to 40 000 eggs a day, but otherwise immobile and helpless, tended by her sterile sisters. What of the parasite *Schistosoma*, a worm that causes the debilitating disease schistosomiasis (otherwise known as bilharzia) among hundreds of millions of people in many tropical countries? The female is larger than the male, and has a groove in which she holds the much smaller male in a continuous embrace, able to fertilize her at any time. Finally, for us who eat a wide range of different foods it is difficult to imagine any animal as specialized as certain kinds of marine snail. These feed by penetrating the individual compartments (called cells) of seaweed fronds with their teeth. So finely matched is the shape of the snail's tooth to the shape of the cells on which it feeds, that each species of snail can feed on one and only one type of seaweed. For none of the other seaweeds do its teeth fit.

As humans we are, naturally, interested in ourselves, and we tend to think of the living world as consisting only of ourselves and those few species of animals and plants that we easily recognize or frequently come across in our daily lives. Although these Units will certainly deal with those aspects of biology that are of human interest, there is far more to the living world than our own species. Indeed, humans seen in the context of the rest of the living world are a relatively rare kind of animal belonging to an obscure and not particularly successful group of animals, the primates, which can between them muster a little over 200 species, in comparison with the 290 000 species of beetles. Biology, therefore, is much more than the study of human beings. It is the study of *all* living organisms: animals, plants, fungi, and other simpler forms—the bacteria and viruses.

2.2 THE CELLULAR NATURE OF LIFE

So far you have seen that living organisms, animals, plants and other forms of life, are very diverse. What happens when we look inside organisms, and investigate their internal structure? Is that diversity maintained, or are there some features that are common to many, or perhaps to all organisms? To answer this, let us explore the bodies of organisms in progressively closer detail.

Inside a human body there are a number of **organs**—heart, lungs, kidneys and brain, for example. An organ is a distinct *part* having particular functions. Other animals have many of these organs, too, and sometimes additional ones such as the gills of fish or the electric organ of electric eels. Plants also have organs: roots, leaves and flowers are familiar examples. But across the whole living world, the number of different organs is fairly limited. Though there is immense diversity in species, the range of different organs is far smaller. The next level of organization within organs is that of **tissues**—muscle and bone are two examples. But bone in one animal is very similar to bone in another, and the same can be said of muscle, skin and so on. As with organs, it is plain that a limited number of structures underlie the enormous diversity of species. However, it is when we look still more closely at animals and plants, when we use a microscope and look at highly magnified slices of animal and plant tissue that a really startling feature emerges. The tissues are made of **cells**. These, as their name implies, are individual units—you can think of them as little boxes—present in the tissue in anything from tens to thousands or millions, depending upon the

MULTICELLULAR

UNICELLULAR

ORGANELLES

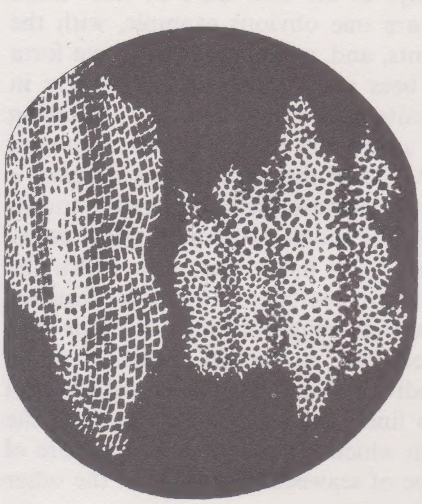


FIGURE 1 The first drawing ever made of cells—by Robert Hooke in 1665.

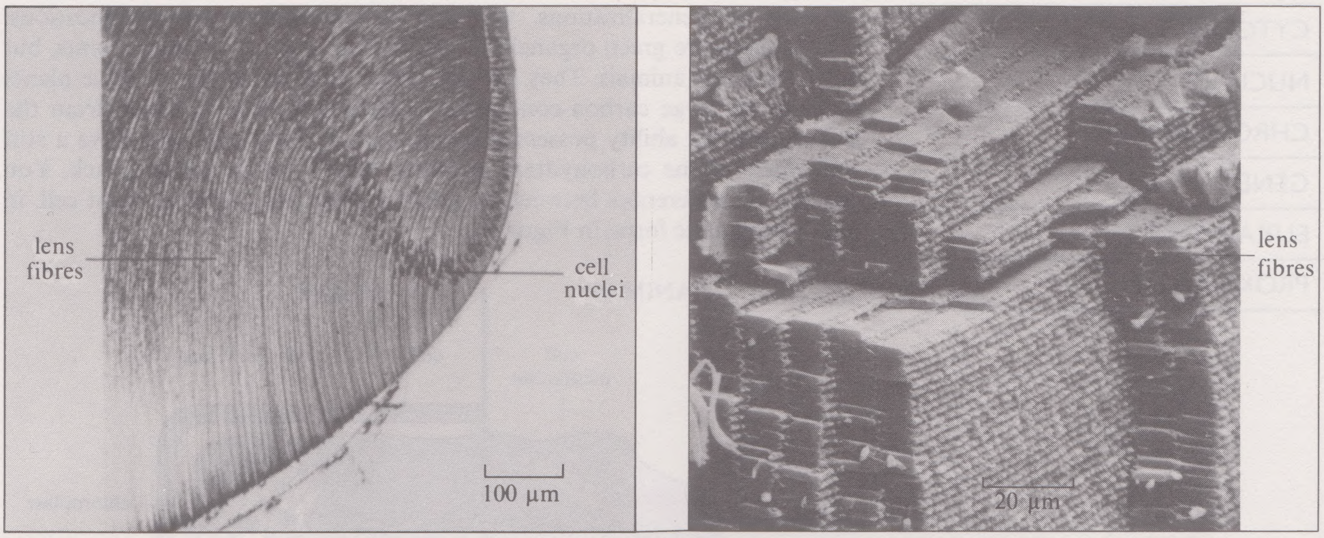
tissue. The human brain, for example, contains about ten thousand million (10^{10}) nerve cells, whereas a newly germinating seedling has just a few hundred cells.

Robert Hooke first used the word 'cell' in a biological sense in 1665 when he saw that the structure of cork (which comes from the bark of a tree) and of pith (which comes from plant stems) was '. . . much like a honeycombe . . . these pores, or cells, were not deep but consisted of a great many little boxes. . . .' Figure 1 shows the drawing that Hooke made of these cells. It was not until many years later, in 1838, that two biologists, Jacob Mathias Schleiden and Theodor Ambrose Hubert Schwann, proposed that 'all living organisms have cells as their basic unit of structure'.

Although large organisms, such as human beings, have many cells in their bodies (the technical term for such organisms is **multicellular**), some small organisms have only one. These **unicellular** organisms (or unicells, as they are sometimes called) are usually too small to see with the naked eye; the slow-moving unicellular animals of pondwater called amoebae, and parasitic versions of these animals that can invade human guts and cause amoebic dysentery, provide examples. Cells vary in size but are usually relatively small. Most animal cells are around 50–100 micrometres across. (One micrometre, abbreviated to μm from now on, is 10^{-6} m.) Plant cells are somewhat larger, perhaps 200–300 μm. Some cells can be very long: the long fibre of a nerve cell in humans can be a metre long, reaching from brain to abdomen, and skin cells of plant stems and leaves can be 1 000–2 000 μm long.

It is not simply the size of cells that is of interest, however; it is their appearance and structure. As you read the biology Units you will come across many different kinds of cell, but to give you a foretaste, look at Figure 2. This shows photographs of several different kinds of cell taken by an instrument called the scanning electron microscope (SEM for short). Notice how different the cells are in their appearance, and how the appearance of the cell seems to be matched to the job that the cell performs in the body. The cells in the lens of the eye, for example, are long fibres that are stacked on top of one another in neat piles (Figure 2a). Each cell contains proteins that refract the light passing through. The combined effect of all these fibres, in the healthy eye, is to produce a lens of high optical quality. The sperm cell has a long tail which drives the sperm towards the egg, a comparatively vast and immobile cell (Figure 2b). The red and white blood cells (Figure 2c) have surfaces that allow them to flow easily through the blood vessels, the red blood cells carrying oxygen towards and CO_2 (carbon dioxide) away from organs, and the white blood cells having an important role in engulfing potentially dangerous objects that invade the body. In plants, too, there are a variety of cells. Just by looking at them, you can almost guess the part they play in the plant's life. For example, the leaves of many plants have pores that regulate the flow of gases between the leaf and the outside air (Figure 2d). Each pore is surrounded by two cells, called guard cells, that can open and close the pore and so slow down or speed up the rate of flow of the gases.

The outside appearance of cells thus seems to be related quite closely to the function that the cells perform. But what lies inside cells? If you look at a cell from an animal or plant under a microscope, it may at first sight seem to be empty, but if it has been stained with dyes or if special microscopical techniques have been used then it becomes clear that the cell is full of interesting structures. Collectively they are called **organelles**, which means 'little organs'. We shall describe them later, but the important point to note here is that the cells of almost all living multicellular organisms—and many unicellular ones, too—contain the same kinds of organelles. There is an underlying uniformity in life at this level which is not present in whole cells or in whole organisms. It is this unity beneath the diversity that makes the living world so interesting.



(a)

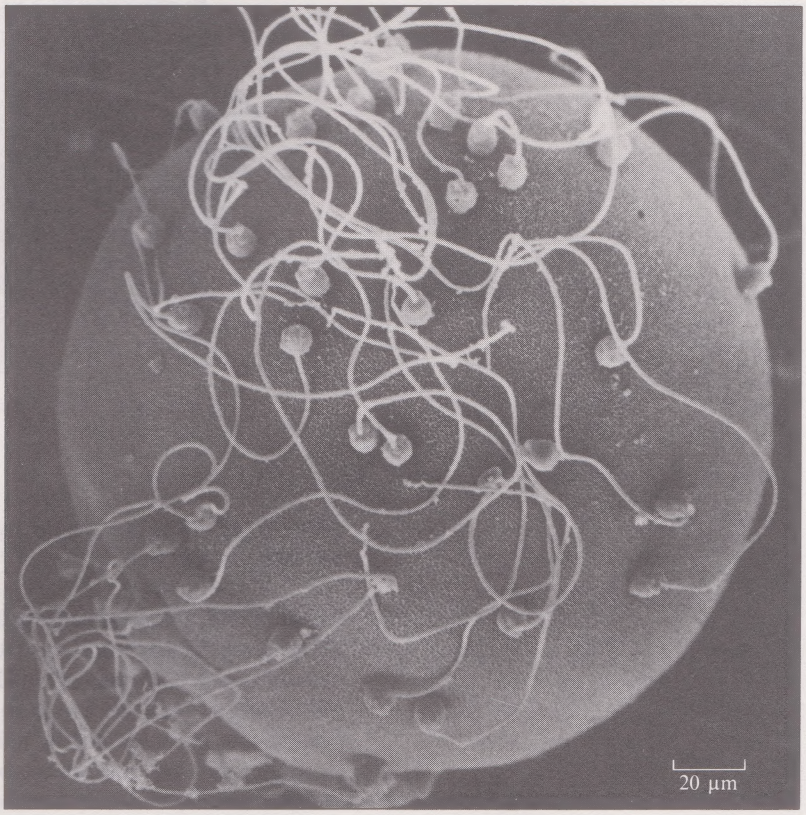
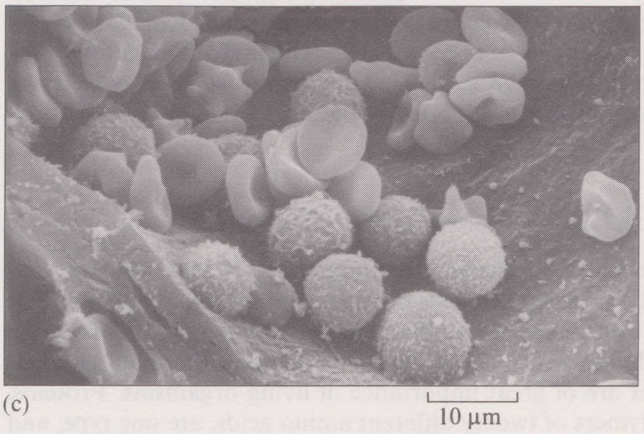
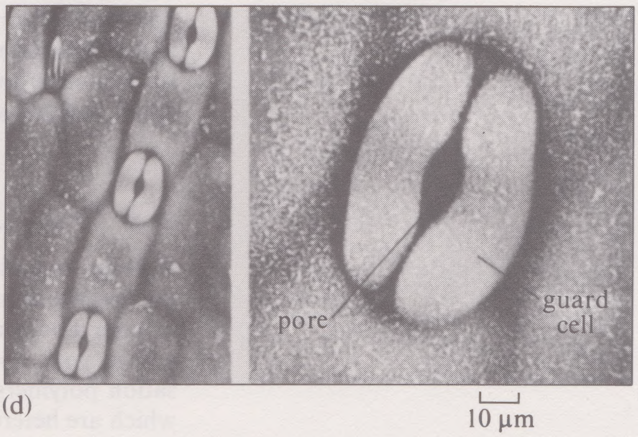


FIGURE 2 Highly magnified photographs of (a) the lens of a human eye; (b) clam sperms and egg; (c) red and white blood cells (the larger, more spherical cells with rough surfaces are white blood cells; the smaller, flatter cells are red blood cells); (d) guard cells in a tropical grass. (Figures 2a (right) and 2c are from *Tissues and Organs: a text-atlas of scanning electron microscopy* by Richard G. Kessel and Randy H. Kardon. Copyright © 1979 W. H. Freeman and Company. Reprinted with permission.)

(b)



(c)



(d)

CYTOSOL

NUCLEUS

CHROMOSOMES

GENES

EUKARYOTE

PROKARYOTE

As with all generalizations, we have to introduce some qualifications. Chloroplasts are green organelles found within the cells of most plants, but not in those of animals. They are associated with the ability of these plants to build up large carbon-containing molecules from CO_2 taken from the atmosphere, an ability possessed by no animal. Plant cells also have a stiff wall made of the carbohydrate cellulose, which, again, animals lack. You can see the differences between a typical animal and a typical plant cell, in highly schematic form, in Figure 3.

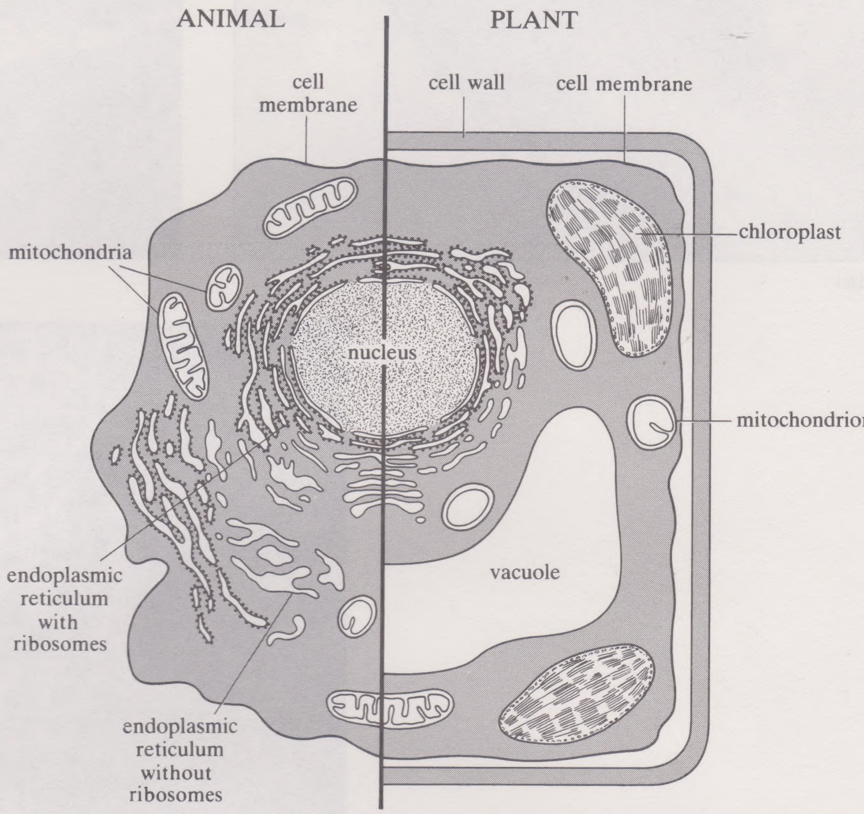


FIGURE 3 A diagrammatic composite showing the principal features of typical animal and plant cells.

Inside a cell, the organelles exist in a broth of chemicals of various types—all of great importance as you will see in Unit 22. The broth is called the **cytosol** and it occupies about half of the cell's volume. During the course of the biology Units we are going to build up a picture of the organelles that float in the cytosol, and to help us we shall refer often to Figure 3 in order to highlight the particular organelle under discussion. To help you to become totally familiar with cellular structure, Figure 3 is printed on the back of each biology binding. In this Unit and in Unit 20 we shall focus on one very important organelle, the **nucleus**, a sac suspended in the cytosol and which occupies about 5% of the total cell volume. To find out why the nucleus is so important we have to look at the living world in even more detail, and investigate the chemical nature of life.

2.3 THE CHEMICAL NATURE OF LIFE

A living organism consists of chemicals. About 80% of you is water, and the balance is mainly organic chemicals of various kinds and a few minerals in your bones and ionic compounds dissolved in the cytosol of your cells and in your body fluids. Units 17–18 described some of the main condensation polymers that are of great importance in living organisms. Proteins, which are heteropolymers of twenty different amino acids, are one type, and nucleic acids, for example, deoxyribonucleic acid (DNA), are another. The word protein from the Greek *proteos* (meaning of first rank), proclaims the importance of this group of molecules. Indeed, life on Earth is sometimes

described as being 'protein-centred'. Proteins play a variety of essential roles in organisms: every reaction in your body is catalysed by a special protein catalyst (an enzyme). Oxygen is carried from your lungs to your tissues by a protein (haemoglobin) in your red blood cells. Each of the thousands of millions of cells in your body has proteins involved in every aspect of its structure and function. Your blood sugar is maintained at its correct level by a protein (insulin), and your body wards off attacks from bacteria by means of proteins (immunoglobulins) of the white blood cells. Proteins are closely linked with DNA in the chemical processes that occur inside the cell. In all plants and animals and bacteria, and in many (but not all) viruses, DNA contains encoded information which substantially affects the nature of the organism. In the human body, for example, every cell nucleus contains 46 thread-like structures called **chromosomes**, made partially of DNA, and the DNA on each thread carries the units of information called **genes**. Together with the effect of the environment, the DNA of your genes contributes to every aspect of your persona—your height, your skin and hair colour, whether you are male or female, your potential for longevity, your intelligence, and your behaviour. How DNA has its effect is plain in a few cases (usually where one gene only is involved) and obscure in others (usually where the effect involves several genes). But, in all cases, the encoded message in the DNA is revealed via particular proteins. A particular kind of protein molecule which does a particular job in the organism is made always by a particular kind of DNA molecule. Usually it does this via another kind of biopolymer called RNA, and biologists often describe the phrase 'DNA makes RNA makes protein' as the central dogma of modern biology.

DNA, as we said, lies on the chromosomes in the nucleus. At least, it does in animals and plants. This is what makes the nucleus so important. Animals and plants, because they have cells with nuclei, are sometimes called collectively **eukaryotes** (pronounced 'you-carry-oats'). Some unicellular organisms, such as various species of amoebae, are eukaryotic also. This distinguishes them from bacteria—forms of life that we have so far only mentioned in passing—where there is *no* nucleus, and indeed there are no organelles at all. These apparently simpler organisms are called **prokaryotes**. Their DNA, RNA, proteins and other molecules all exist within the single compartment of the cell. Bacteria are of the order of 1–10 μm long, and reproduce themselves simply by splitting into two, sometimes as often as once every 20 minutes. Bacteria are very important. Nitrogen-fixing bacteria live in nodules on the roots of beans, peas, clover, and many other plants, and are able to convert or 'fix' atmospheric nitrogen into ammonium ions that can then be used by the host plants for nutrition. Other bacteria are now used commercially to convert oil to cattle feed. Bacteria also rot and digest animal corpses, and carry infection and diseases.

Viruses are different. They are of the order of 0.1–0.5 μm long and do not have a completely independent life of their own, but reproduce within animals, plants and bacteria. They, too, carry diseases such as influenza and AIDS.

2.4 THE LIVING WORLD: DIFFERENT LEVELS OF INVESTIGATION

Sections 2.1 to 2.3 have made you look at the living world in four different ways: at the diversity and huge numbers of whole organisms; at the level of a single organism; at the cells that form the building blocks of these organisms; and finally at the chemical events that occur in organelles within the cells.

You might wonder whether one of these ways of looking at the living world is better than or more important than any of the others. Do we obtain a truer picture of biology by studying proteins and DNA, by looking at the cells of leaf or kidney, by considering an elephant or a wasp, or a whole field of dandelions? The answer is that all four ways of looking at life are equally important. To leave out one, or overemphasize another is to impov-

SYNTHESIS
REPLICATION
REPRODUCTION
GAMETES
GERM CELLS
EVOLUTION
DARWIN'S THEORY OF EVOLUTION BY NATURAL SELECTION

erish our understanding. An animal or plant is not simply a pile of chemicals, and one can never understand how it functions in the real world if one only studies the chemical reactions that go on inside its cells. Conversely, one can never understand fully how an organism functions in the real world unless one knows about the chemical and other events that are happening inside its tissues, cells and organelles. For this very reason you will find that the following Units jump backwards and forwards from organisms and whole populations of organisms to cells, from cells to chemicals and organelles, from organelles to tissues and organs, and so on. We hope that you will find the order in which we cover the various areas of biology logical and clear, but it may help you if you have constantly at the back of your mind these different levels of investigation, and also what can be called the fundamental processes of life.

2.5 THE PROCESSES OF LIFE

At the end of Units 17–18 you read about various kinds of giant molecules, the proteins and polynucleotides. They are not only important in the daily lives of organisms, but on their own possess rather lifelike properties. Under the right laboratory conditions, amino acids will form condensation polymers—protein molecules that will continue to grow in size and complexity until the polymerization stops. And yet neither proteins on their own nor DNA on its own are alive. What exactly must a collection of proteins, polynucleotides and other chemicals *do* to qualify as living? Here we are asking not so much what structures (like cells or teeth) living things have, as what unique processes go on inside them.

□ From what you have read so far, suggest one distinctive process that goes on only in living organisms.

■ The process DNA-makes-RNA-makes-protein is found in nearly all forms of life. (Only in some viruses, where RNA is present instead of DNA, is this not the whole story.)

This ability of DNA to direct, via RNA, the production (**synthesis**) of proteins, which in turn can control the synthesis of all the other chemicals in the body, is one of the key processes of life. There are several other key processes, but we shall concentrate upon just two. These are the ability to replicate (**replication**) and the ability to reproduce (**reproduction**). To replicate is to produce an exact copy. Scientists often attempt to replicate each others' experiments, trying to copy as exactly as possible the conditions under which the original experiment was performed, to see whether they get the same result. All living organisms have a component which can be replicated: in almost all of them it is DNA. When a human baby is developing from a fertilized egg, its cells are dividing time and time again to give two, four, eight and ultimately thousands of millions of cells in the body. Each time a cell divides, the DNA in its nucleus is copied exactly with the result that the newly-formed cells carry copies of DNA identical to the DNA that was present in the cell from which they were formed.

Not only do living organisms have components that can replicate, the organisms themselves can also reproduce. Reproduction is different from replication. To reproduce is to leave descendants. You are a product of your mother's and father's reproduction. You are not an exact copy of either of them. You are the product of the fusion of two simple cells, an egg cell and a sperm cell, collectively called **gametes** or **germ cells**, from which you, a complex organism, have developed. You in turn may already have reproduced, or may do so in the future. The characteristic feature of reproduction, then, is the repeated sequence of events that can be represented as follows:

$$\text{adult} \longrightarrow \underset{\text{(egg or sperm)}}{\text{germ cell}} \longrightarrow \text{adult} \longrightarrow \underset{\text{(egg or sperm)}}{\text{germ cell}}$$

Replication simply produces more of the same: more cells leading to a bigger body. Reproduction leads to the formation of completely new bodies.

We emphasize these three features of life—synthesis, replication and reproduction—because they will keep reappearing in Units 20–26. For example, reproduction is central to *Darwin's theory of evolution by natural selection*, to which you will shortly be turning. But it turns out that also central to his theory is the way in which genes affect the appearance and functioning of organisms, that is, the way in which DNA controls the synthesis of proteins that in turn affect the appearance and functioning of the organism.

You may remember from our discussion of cells in Section 2.2 that we emphasized the way in which the structure of a cell can match the role that the cell plays in the animal's or plant's life. This idea of matching structure to function turns out to be a key concept in biology, not only at the cellular level, but at the level of molecules and, particularly, of whole organisms. As we leave this overview of biology you should carry this idea forward into the beginning of the next Section, where we start our exploration of biology in depth. It is the starting point for understanding Darwin's theory of evolution by natural selection. And that, by the time we reach Unit 21, should explain why and how there is such a diversity of species on our planet.

SUMMARY OF SECTION 2

1 There has been life on Earth for around four thousand million years. Life is enormously diverse, with millions of different kinds (species) of organism currently existing. Despite this diversity, there is an underlying unity in terms of cellular and chemical structure.

2 Apart from viruses (which reproduce inside other cells) all organisms are built of cells. Some organisms consist of just one cell (unicellular organisms) but others consist of many cells (multicellular organisms).

3 All multicellular and some unicellular organisms have cells that contain separate structures called organelles: one such is the nucleus. Cells with true nuclei are called eukaryotic cells. Bacteria, apparently primitive unicells, have no true nuclei and are called prokaryotes.

4 Two important groups of cellular chemicals are the proteins and the nucleic acids. DNA is contained in genes within chromosomes—and, through proteins, influences the nature of organisms. DNA molecules are replicated as new cells are formed. The production of new DNA is replication but the production of new organisms is reproduction.

3 EVOLUTION

We begin our study of biology with one of the most fundamental characteristics of life, and one of the greatest ideas in science. The phenomenon is **evolution**, and the idea is **Darwin's theory of evolution by natural selection**.

Before about 4 000 million years ago there was no life on Earth, but now there are millions of different kinds of organisms ranging in structure from the simplest viruses to the most complicated flowering plants, insects and mammals. During this period, the kinds of organisms in existence have changed dramatically. These changes are described in detail in Units 28–29. Whole groups of organisms have flourished and then become extinct, like the dinosaurs that were on the Earth from 200 million until 65 million years ago.

In general, as time has passed, the structure of animals and plants has become more complicated. For example, insects, with their astonishingly elaborate eyes and very efficient flight muscles, have been on Earth for only 130 million years, as have the flowering plants. Humans and their immediate ancestors have been on Earth for only the last two million years or so.

PALAEONTOLOGY

ACQUIRED CHARACTERISTICS

ADAPTATION

The process by which these changes have occurred over time is termed evolution, and the branch of science concerned with the study of biological events in the past is known as **palaeontology**.

It is one thing to describe the historical course that evolution has taken; it is quite another to explain what has been *responsible* for these evolutionary changes. What causes evolution to happen is one of the major questions that have confronted biologists over the past two hundred years. Those who study the causes of evolution are sometimes referred to as evolutionary biologists, the most famous of whom was Charles Darwin (Figure 4).

FIGURE 4 Charles Darwin in 1860, aged 51. This portrait was taken about the time that his theory of evolution was published.

The idea that animals and plants have evolved is not new and can be found in the writings of some of philosophers of Ancient Greece. However, it was not until the 18th and 19th centuries that people's interest in evolution really began to flourish, and they began to develop explanations about the causes of evolution. Foremost in promoting this interest was the French naturalist Jean Baptiste Lamarck (1744–1829) who was responsible for the first major theory as to the mechanism by which evolution works. His theory was that the *characteristics* that an animal or plant *acquires* as a result of the kind of life it leads and as a result of the way in which the environment acts upon it *can be passed on* to the next generation. If an antelope-like animal, so the well-known example goes, habitually stretches its neck to reach the juiciest leaves at the tops of trees, then during the course of its life, its neck will grow longer. It will pass on this long-necked characteristic to its offspring, who will do the same, and after generations its descendants will have evolved into giraffes.

Lamarck's theory (concerning, as it did, these **acquired characteristics**) fell from favour, in part because it was realized that these characteristics are not passed on in this way. It was superseded by a theory that has become one of the best-known and most important in modern science: the theory of evolution by natural selection, also known as Darwin's theory of evolution. The name 'Darwin's theory' is perhaps an example of historical unfairness as the theory was developed separately but simultaneously by two naturalists, Alfred Russel Wallace and Charles Darwin. However, it is with the latter that the theory is most closely associated.

The theory of natural selection can be stated in a few lines, as follows:

1 The individual characteristics of an organism—its height, colour, quickness to react, and so on—are vitally important for its survival and its reproductive success.

2 Individuals of a given kind of organism—take beech trees as an example—vary in these characteristics. Individuals with certain characteristics—beech trees that are more resistant than other beech trees to fungal attack—do better than individuals lacking those characteristics. They tend to live longer and leave more offspring.

3 Because the world cannot support all of the offspring produced by organisms, only a small proportion of them survive. If the features that help certain individuals to survive and reproduce better than others are passed on by inheritance to offspring by their parents, then individuals with those features will become more common as the generations pass by at the expense of individuals without those features. This is the basis of evolutionary change.

This brief summary of the theory of evolution by natural selection does not do justice to it, nor does it allow you to judge for yourself its importance. Darwin's theory has profoundly influenced biological thought over the past hundred years, and to show why this is so we have to investigate it in some detail. This involves discussing a number of key concepts and observations about living organisms. These are adaptation, fitness, inheritance, competition and selection. By the end of the Unit it should become clear, from the way in which living organisms reproduce and the way in which replication takes place, that two of the three attributes of living organisms emphasized in Section 2.5 are central to Darwin's theory.

3.1 ADAPTATION: THE RELATIONSHIP BETWEEN STRUCTURE AND FUNCTION

The structure and appearance of an organism often seem very well suited to the kind of life that the organism leads. One of the achievements of the theory of natural selection is to explain why this is so—why, to use the technical term, organisms appear to be adapted to their environment (or, put another way, why they exhibit **adaptation**). It is a measure of this achievement that biologists since Darwin almost automatically try to relate the structures they are studying to the functions of those structures in the animal's or plant's life. The following examples illustrate the idea of adaptation: that is, the notion that there is a close relationship between structure and function.

Example 1

Note Plates 1–10 are at the end of this binding.

Consider the fact that most kinds of animals are eaten by other animals called predators. Many kinds of insects seem to human eyes to be particularly well-camouflaged. Plate 1 shows a stick insect on a fairly uniform brown background, and Plate 2 shows the same insect against a background of twigs and leaves. The fact that the insect's body and legs are so twig-like in appearance makes it difficult to see in its natural surroundings. Moreover, animals that are well camouflaged, like stick insects, often behave in such a way as to make themselves still less visible to predators. They tend to remain motionless in the presence of a predator, often concealed beneath a mass of foliage. By contrast, many kinds of animals that are not usually subject to predation are not camouflaged. They tend to be brightly coloured and to move about openly. Often, also, they have some defence mechanism such as a sting. Bees and wasps are obvious examples.

Example 2

Some of the most striking examples of adaptations are found when one examines several different kinds of organism that live under similar environmental conditions. For example, there are several different kinds of large animal that live in the sea and are good swimmers. Figure 5 (overleaf) shows some of these animals.

□ Which two features that seem to be adaptations to a way of life in which swimming plays an important part do all these animals have in common?

■ There are two main features. The first is that all of them have smooth, torpedo-shaped bodies. This is the shape that marine engineers have discovered meets with rather a low water resistance (in comparison with bodies of other shapes) when it moves through the water. The second feature is that they all have fins or flippers and tails that drive them through the water. The flippers of the porpoises are in fact their front legs, and look rather like fish fins; they are totally unlike the front limbs of other mammals, for example, monkeys or rats. A penguin's flippers are, of course, its wings, and again are not at all like the wings of, say, starlings or rooks. Notice also that the porpoises do not seem to have any back limbs at all. There are a few tiny bones hidden below the surface of the body, with the result that the contour of the animal towards the back is smooth, just as it is in the fish. Notice finally that all of them have paddle-like structures at the back of the body.

The animals shown in Figure 5 come from quite different groups, despite their superficial similarities. Porpoises and seals are mammals: that is, they belong to a group of animals (to which human beings also belong) that are unique in suckling their young and having hair covering part or all of their skin. Perch and dogfish are fish, although they come from very different groups; perch from a group with bony skeletons, and dogfish from a group

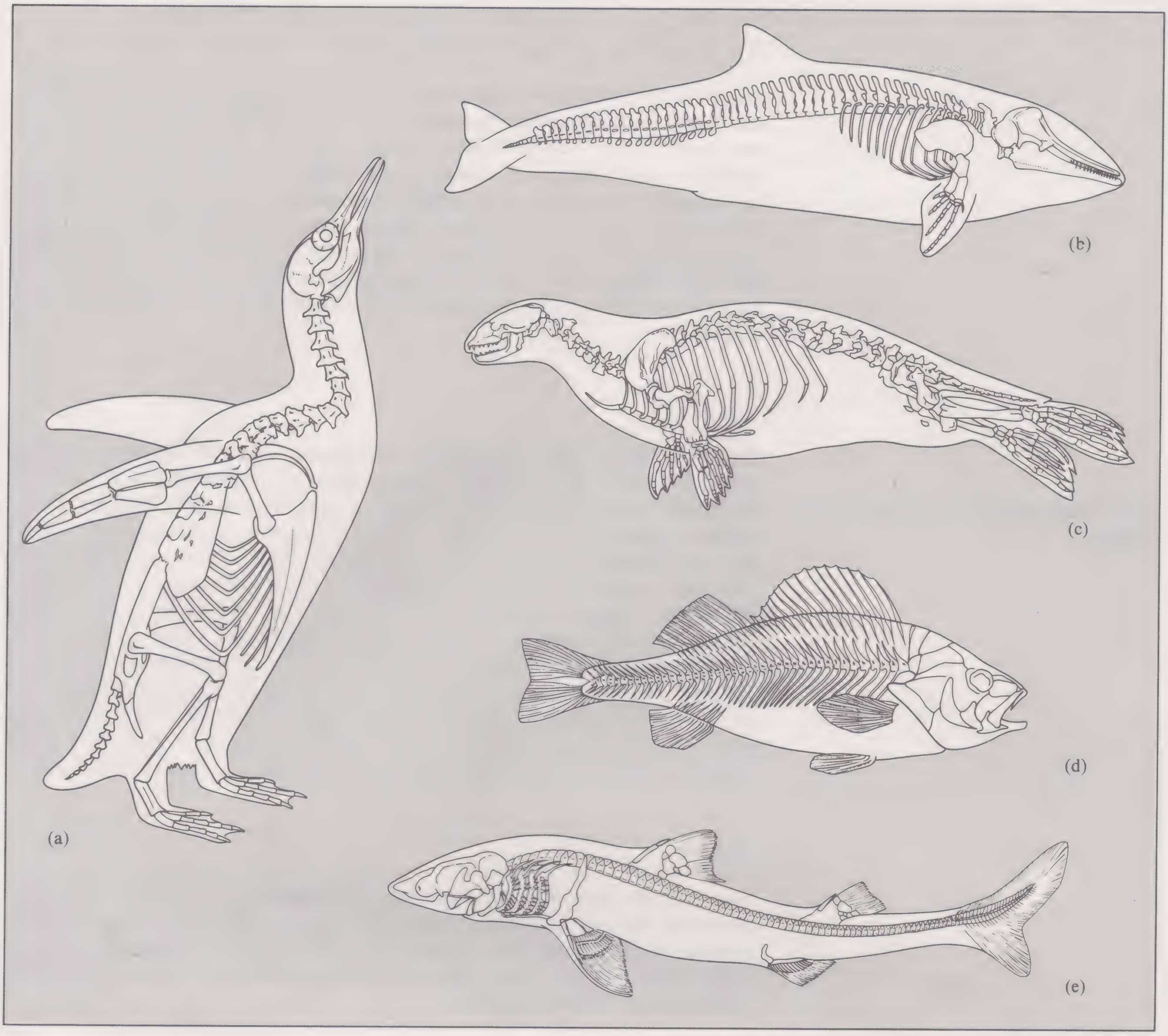


FIGURE 5 The body outlines and skeletons of five aquatic animals (not to scale): (a) a penguin; (b) a porpoise; (c) a seal; (d) a perch; (e) a dogfish.

MORPHOLOGY

CONVERGENCE

containing sharks and rays that have skeletons made of cartilage (the flexible material that also strengthens the human ear). Penguins, of course, are birds; a group that is unique in the possession of feathers. The basic design of mammals, birds, bony and cartilagenous fish—the **morphology** as it is called—is therefore very different. Despite this, the animals shown in Figure 5 resemble each other in just those features—the streamlined shape and flippers or fins—that are useful for an aquatic life. Moreover, mammals and birds that are not aquatic do not show these features. All this provides strong evidence that the streamlining and the possession of flippers or fins are adaptations to an aquatic way of life. The phenomenon of organisms with very different basic morphologies sharing superficial similarities in features that relate to a common way of life is known as **convergence**. Examples of convergence are very common among animals and plants, and provide strong evidence that the convergent features are indeed adaptations to the environment, and not fortuitous accidents.

So far, the arguments put forward about this or that feature being adaptive have been purely intuitive; no experimental evidence has been quoted. If the study of adaptation is to be at all rigorous, then it is important to decide upon some criteria for determining whether a particular morphological feature is adaptive or not. This issue is discussed in Section 4.

SUMMARY OF SECTION 3

1 The first major theory to try to explain the cause of evolution was Lamarck's theory of the evolution of acquired characteristics. This failed because modern research into mechanisms of inheritance suggests strongly that acquired characteristics are not inherited. It was superseded by the theory of evolution by natural selection, developed by Darwin and Wallace.

2 A key concept in the theory of natural selection is adaptation. The structure and appearance of organisms, that is their morphology, appears to be well suited to their way of life.

3 Strong evidence for adaptation comes from the phenomenon of convergence, whereby organisms with different basic morphologies share superficial similarities in features that relate to their common way of life.

SAQ 1 Choose from the following options (a)–(e) the one that provides a correct description of convergence.

(a) Groups of animals or plants are said to show convergence if they possess different morphological features even though they live in the same environment.

(b) Mammals are said to be convergent with fish and birds because representatives of each group are capable of swimming.

(c) Groups of animals or plants are said to show convergence if they possess similar morphological features even though they live in different environments.

(d) Certain mammals, fish and birds are said to show convergence if they have superficially similar morphological features even though they live in different surroundings.

(e) Certain mammals, fish and birds provide an example of convergence; that is, they have superficially similar morphological features that are adaptations to similar modes of life.

SAQ 2 What is meant by a morphological feature of an organism?

SAQ 3 Many bats hunt moths by echo-location rather than by sight. That is, the bats emit high-pitched pulses of sound that bounce back off passing objects (including insects). The bats are able to assess the location and certain other features of the objects in their surroundings from the quality of the echoes that they pick up.

Which of the following features of moths would seem to be adaptations related to their being hunted by bats?

(a) Cryptic coloration that camouflages the moth.

(b) Possession of organs that are very sensitive to sound.

(c) Possession of well-developed eyes.

(d) An escape routine that is performed whenever high-pitched pulses of sound are heard.

4 ADAPTATION AND SURVIVAL

This Section describes an important piece of research in which it was shown that organisms differing in their outward appearance differed also in their ability to survive. Two new terms, phenotype and fitness, are then introduced, which are central to the theory of evolution by natural selection.

If a feature is adaptive, one would expect an organism possessing that feature to have a better chance of surviving than an organism that lacks it. For example, if a stick insect's stick-like shape is adaptive in the sense that it helps to conceal the insect from predators, then one should predict that fewer stick insects should be eaten by predators than insects that are similar but not stick-like. Similarly, if the squat, dumpy shape of a cactus plant is

thought to be adaptive in the sense that it protects the plant from drying out under desert conditions, one would predict that such a cactus should have a better chance of survival than a plant similar to it but lacking the squat, dumpy shape. Notice, however, that in both examples just quoted, the stick insect and the cactus, the element of comparison is stressed.

☐ Why should comparison be important? What problem does such a comparison pose?

■ To be certain beyond any doubt that a particular morphological feature aids survival, it would be necessary to compare the ability to survive of organisms that are *identical except in the one feature of interest.* If the organisms were to differ from one another in other features as well, it would be impossible to say that any difference in ability to survive was due to the feature in question rather than to one or more of the others in which the organisms differed. (This is just the same problem as is encountered in many other branches of science. If you want to investigate the effect of a particular factor, whether it is the effect of temperature on the rate at which a chemical reaction proceeds, or the effect of body colour on survival, you need to control those factors whose variation might confuse matters, for example, the concentration of the reactants, atmospheric pressure, the type of environment in which the animal is being studied, etc.)

Usually, it is just not possible to make such a rigorous comparison. How, for example, could one possibly find a stick insect that is identical to another in every respect, except that it lacks stick-like features? Equally, how could one find a cactus that is identical to the cactus in question but is not squat and dumpy? In fact, biologists usually have to depend on more indirect ways of assessing whether or not a particular feature is truly adaptive. In the stick insect example, such a way might be to compare predation rates of birds on the insects in their natural 'twiggy' environment with insects placed in a 'bare' artificial environment. The key thing, however, is to avoid untested intuition. It may be a splendid idea to suppose that the pinkness of flamingoes is an adaptation—on the grounds that the colour affords camouflage when the birds are viewed against the pinkness of sunsets. Alas there is not a ha'p'orth of evidence to support it!

Sometimes, however, it *is* possible to carry out a very direct comparison between organisms that differ in one particular feature only. One of the best known of these investigations was begun by H. B. D. Kettlewell in the 1950s, and has since then been carried on by Kettlewell and by several others. The work was carried out on a moth that is common in Britain, the peppered moth. (Its scientific name is *Biston betularia.* There is no need to remember it; biological nomenclature will be discussed in Unit 21.) There are three different colour forms of this moth. One, called the typical form, is pale and speckled. Another, called the *carbonaria* form, is a sooty black. The third is intermediate in colour between the other two: it is black with patches of white, and is known as the *insularia* form. The three colour forms are shown in Plates 3, 4 and 5. For the moment, let us concentrate on the typical and the *carbonaria* forms; *insularia* comes into the story later on.

The moths are active at night and settle during the day on the bark of trees. In rural parts of Britain, where the air is clean, the bark of trees is paler than in the sooty areas of industrialized towns. One reason for this is that there is less soot deposited on the bark of trees in the country than in industrial towns. Another reason is that fewer lichens and other small plants grow on tree trunks in industrial areas because the high concentration of sulphur dioxide in the air prevents their growth. These small plants are usually pale green or white in colour (Plate 6). Viewed against a background of bark of a tree from a rural area, the pale form of the moth is, to the human eye rather difficult to see, whereas the black form is very obvious (Plates 7 and 8). On the other hand, when viewed against the bark of a tree from an industrialized area, exactly the reverse is true; the pale form stands out, and the *carbonaria* form is nearly invisible (Plates 9 and 10).

Moths of both colours are eaten by birds such as robins, nuthatches and thrushes. It is therefore natural to ask whether these birds find pale moths more conspicuous than dark moths against a dark background and vice versa, just as they are to us. Kettlewell used three different methods to investigate whether the colour of the moths made any difference to their ability to survive. He used each method in two localities, one a suitably filthy patch of woodland near Birmingham and the other an unpolluted woodland in Dorset.

Method 1

Equal numbers of the typical and *carbonaria* forms were released onto tree trunks and branches in the woodlands. The moths were then watched, and the numbers of each colour form that were eaten were recorded. Whenever, during the course of a day's observation, all the moths of one particular colour form had been eaten, more of that colour form were put out on the trees. The numbers of the different colour forms that were eaten in the two localities are shown in Table 1.

TABLE 1(a) Number of peppered moths eaten by redstarts during two days of observation in a wood near Birmingham

	Typical	*carbonaria*	Total
19 July 1955			
a.m.	12	3	15
20 July 1955			
a.m.	14	3	17
p.m.	17	9	26
total	43	15	58

TABLE 1(b) Number of peppered moths eaten by five different kinds of birds in a Dorset wood

Bird	Typical	*carbonaria*	Total
spotted flycatcher	9	81	90
nuthatch	11	40	51
yellowhammer	0	20	20
robin	2	12	14
thrush	4	11	15
total	26	164	190

Method 2

Kettlewell captured moths in the woodlands and counted how many *carbonaria* and how many typical forms were present in the catch. He used two different methods of capturing the moths in each locality. One was a light trap, consisting of a fluorescent bulb that attracts moths which then settle in a tub placed underneath the bulb. The other was what is known as an assembler trap. Females are put in a small gauze container and the odours from the females attract the males who cluster around and can then be netted. On some nights he operated both methods of trapping simultaneously. The numbers of each colour form that he caught in each locality on those nights are shown in Table 2.

TABLE 2 Numbers of different colour forms caught by two methods of trapping in two localities

(a) Birmingham	Light trap		Assembler trap	
	typical	*carbonaria*	typical	*carbonaria*
1953	47	263	34	281
1955	25	167	30	255

(b) Dorset	Light trap		Assembler trap	
	typical	*carbonaria*	typical	*carbonaria*
1955	166	14	193	20

PHENOTYPE

FITNESS

Method 3

Moths that had been reared in cages were marked with small spots of paint so that they could be recognized if they were recaptured. They were then released into the woodland in the two localities. Over the following days some of these moths turned up among those caught either in the light traps or the assembler traps. The numbers of the different colour forms that were released and the numbers that were recaptured are shown in Table 3.

TABLE 3 Numbers of different colour forms recaptured after being released, in two localities

	Numbers released		Numbers recaptured	
(a) Birmingham	typical	*carbonaria*	typical	*carbonaria*
	64	154	16	82
(b) Dorset	typical	*carbonaria*	typical	*carbonaria*
	393	406	54	19

Now work through the following questions on the results of these three methods.

□ From the evidence from method 1, what is the effect of the moth's colour on its chances of being eaten by a bird?

■ In both localities, it is the more conspicuous colour form that is eaten in the larger numbers.

□ Why do you suppose the supply of one particular colour form was replenished when all the moths of that colour were eaten? What effect would this replenishment have had on the results?

■ If the supply had not been topped up, then it is quite likely that after the birds had eaten all of the more conspicuous moths they would have turned to the less conspicuous ones, and would have eaten them too. If this had happened, the numbers of less conspicuous moths eaten would gradually have risen, and might eventually have come to equal the numbers of the more conspicuous moths eaten. By continuing to top up the supply of the more conspicuous form, it was possible to be certain that there were always both colour forms available for the birds.

□ Are there any drawbacks to method 1? That is, is there anything about the method that makes one doubt its results?

■ It could be that it is easier for the observer to see a conspicuous moth being eaten than an inconspicuous one. It is therefore possible that these figures underestimate the number of inconspicuous moths eaten. This is why it is important to use other methods in addition to method 1.

□ What does the evidence from method 2 tell us about the effect of the moth's conspicuousness on its chances of surviving?

■ Table 2 shows that the inconspicuous form is much more numerous than the conspicuous form in both localities. Although these figures on their own do not show that the inconspicuous form is more successful at avoiding predation by birds than the conspicuous form, when taken together with the results of method 1, this explanation looks very plausible.

□ If one is to assume that the figures presented in Table 2 accurately reflect the proportions of the different colour forms in each woodland, what assumption does one first have to make?

■ It has to be assumed that a typical moth is just as much attracted to a light trap or an assembler trap as a *carbonaria* moth and so has an

equal probability of being caught. If the probability that an individual will be caught is influenced by its colour, then the results of method 2 would be more difficult to interpret.

□ What evidence is there from Table 2 that the trapping methods do in fact give a fair reflection of the proportion of the two colour forms in the woodlands?

■ Both trapping methods used in the one locality give rather similar proportions of the two colour forms. In the Birmingham area, the average ratio of *carbonaria* to typical forms is about 6 : 1 from the light trap and about 8 : 1 from the assembler trap. In the Dorset woodland, the equivalent ratios are about 1 : 12 and 1 : 10, respectively. Suppose, for the sake of argument, that *carbonaria* moths were more attracted to the light than typical moths; it would be unlikely that they would also be more attracted to assembler traps. In short, it is possible to be more confident in the results of two different methods of trapping moths than in the results of just one method.

Examine the quantitative evidence from method 3 by trying this ITQ. You should check the answer before continuing.

ITQ 1 From the evidence from method 3, what is the relationship between a moth's ability to survive and its conspicuousness? (You will need to calculate what percentage of the moths of each colour released are recaptured; for example, in Birmingham 64 typicals were released and 16 were recaptured: that is, one-quarter (16/64) or 25% were recaptured.)

□ Is there any evidence from the three methods that *carbonaria* moths are less well adapted to the Dorset woodland than the typical form is to the Birmingham woodland?

■ There are at least two lines of evidence that support this. The results of method 1 show that in the Birmingham area, about three typicals are eaten for every one *carbonaria*, whereas in the Dorset area about six *carbonaria* are eaten for every one typical. Second, Table 2 shows that the ratio of typical to *carbonaria* trapped in Dorset is about 10 or 12 to 1, whereas in the Birmingham area the ratio of *carbonaria* to typical is about 7 or 8 to 1. That is, there is a greater predominance of typicals in Dorset than of *carbonaria* near Birmingham.

The main conclusion that can be drawn from Kettlewell's studies, therefore, is that peppered moths whose colour contrasts with their background survive less well than peppered moths whose colour merges with their background.

It is this kind of rigorous investigation that allows one to speak with some confidence about a particular feature of an organism being adaptive. In this case it is possible to say that the typical form is better adapted to life in the clean Dorset woodland and the *carbonaria* form is better adapted to the polluted woodland near Birmingham.

Before concluding this Section, two new terms need to be introduced. The first is **phenotype**, a word that has two different shades of meaning. First, it can mean the sum of all the characteristics that an organism possesses, not only the morphological, but also the physiological and biochemical features of an organism. For example, two people who are not identical twins will have different phenotypes: they may be of different height, weight, sex, eye colour, blood group, and so on. Second, the word can be used as a synonym of the word 'form' and concentrates, therefore, on one rather than many characteristics. Instead of talking of the *carbonaria* form or the typical form, one can talk of the *carbonaria* phenotype or the typical phenotype. This Unit uses the word in this second sense.

The other important term is **fitness** and it is closely linked with the idea of survival. Its meaning becomes clear if we consider again part of Kettlewell's

EXPONENTIAL GROWTH

work. He showed that moths with different phenotypes from the same locality had different chances of survival. In general, an organism's ability to survive has a direct bearing on its ability to produce offspring; the longer the organism lives, the more likely it is to reproduce. Most organisms have an initial period of immaturity, during which they cannot reproduce. Consequently, if an organism dies shortly after birth, or at any time before maturity, then it will not reproduce. Some organisms, once mature, produce only one generation of offspring and then die (e.g. many insects and annual flowers), others, including human beings, go on reproducing over a considerable period of their lives. In general, therefore, if an organism is to reproduce, it has to survive for at least a minimum length of time and, on top of that, in many organisms the longer it survives after reaching maturity the more offspring it will leave. It should be evident that survival and the ability to produce offspring are closely linked. As a consequence, variations in phenotype that affect an individual's ability to survive will influence its ability to leave offspring as well. These offspring will, of course, eventually mature and produce offspring of their own, provided they survive long enough to do so. What is needed is a word that means 'the ability of an organism to survive and produce offspring that themselves can survive and produce offspring'. *Fitness*, the term introduced at the beginning of this paragraph, is used in this special sense, and you should note that this definition is different from the meaning used in everyday speech to denote good physical condition.

To return to the peppered moth: if it is assumed that phenotypes with a lower probability of survival are likely to raise fewer offspring to maturity than phenotypes with a higher probability of survival, then it is possible to conclude that the different phenotypes in one particular locality *differ in their fitness.*

SUMMARY OF SECTION 4

1 To show that a feature is adaptive requires rigorous, quantitative experimentation on organisms in their natural surroundings.

2 Kettlewell's study of the peppered moth *Biston betularia* is an example of a rigorous study of this kind. He showed that a larger number of conspicuously coloured than inconspicuously coloured forms of the moth were eaten by birds, that inconspicuous forms were more numerous than conspicuous ones, and that they were more likely to survive the period between release and recapture by the experimenter. These results held true whether the moths lived in clean or dirty environments.

3 The peppered moth provides an example in which two phenotypes differ in their fitness.

SAQ 4 A biologist investigates the different colour forms found in a particular kind of mouse. The mouse lives in a variety of localities and eats seeds and roots. 100 mice are captured from an area of sandy heath: 70 are light brown in colour and 30 are grey. In another locality, covered with grey slate, 100 of the same kind of mice are captured: 20 are found to be light brown and 80 grey.

List two assumptions that have to be made if one is to argue that the colour of the mice is adaptive.

Read the answer to SAQ 4 before attempting SAQ 5.

SAQ 5 How would you test whether the second assumption given in the answer to SAQ 4 is true?

SAQ 6 Give an example of an organism whose ability to survive beyond the birth of its offspring might be expected to affect the fitness of the offspring.

5 FITNESS: VIABILITY AND FECUNDITY

The previous Section mentions the word 'survival' many times, particularly with respect to the chances of an organism being eaten. Other factors besides predation threaten an organism's chances of survival, and hence its fitness. These are discussed in this Section and lead the way to a more sophisticated analysis of fitness.

For most organisms, an individual's chance of surviving until it is mature enough to reproduce is either small or very small. A mature oak tree, for example, produces large numbers of acorns, and yet most acorns do not germinate, and only a fraction of the acorns that do germinate grow to maturity and themselves produce acorns. It has been estimated that a female cod produces in her lifetime about nine million eggs. If every one of these eggs were fertilized and developed into an adult, and if half of these adults were females then a single mother cod would give rise to four and a half million females, each one capable of producing another nine million fertilized eggs. If this process were to continue unchecked, after only three generations the entire surface of the world would be covered more than 1.5 kilometres deep in cod.

□ Does this generalization about the low chances of an organism's surviving to maturity apply to humans?

■ At first sight it might seem that it does not. After all, in Britain, the great majority of babies born do survive to maturity. However, this high probability of survival is something that has been achieved only within the last century and is the result of improved medical and child-care practices coupled with an overall improvement in the material standard of living. There are many parts of the world where medical and public health services are rudimentary, food is scarce, and the infant and child death rate is still high.

It is possible to describe in a quantitative rather than a purely qualitative way, how the numbers of organisms of the same kind living in a locality would be expected to increase if unchecked. Some of the calculations are simple. Suppose, for example, an organism were to produce two offspring by laying two eggs or producing two seeds, and then died. (The argument would be the same in principle if one considered a male and female pair that between them produced four offspring; but the argument is easier to follow if this complication is avoided.) Suppose that each of the offspring in turn produced two offspring before dying.

ITQ 2 (a) Work out the numbers of organisms that would be present in each successive generation, and then plot these on the graph paper in Figure 6 (overleaf). (As you can see from the axes, the original single parent is described as 'generation 0'.)

(b) Can you see any arithmetical rule that relates the size of the population to the generation number (0, 1, 2, 3, etc.)?

Growth in which a quantity always *increases* by a fixed factor in a given interval is called **exponential growth**. In this particular example, the population doubles in each successive generation. You met *exponential decay*, the converse of this, in connection with radioactive decay in Units 11–12.

The example that you have just worked through in ITQ 2 is a simple one, compared with what happens with many kinds of organisms. For instance, it requires more effort to calculate how numbers will grow in successive generations in organisms in which the generations overlap—that is, the parents survive after the offspring are born. It is not very difficult to show, however, that the growth in numbers accelerates in such cases as well. (If you wish to verify this for yourself, try SAQs 12 and 13 at the end of this Section.)

POPULATION

FECUNDITY

VIABILITY

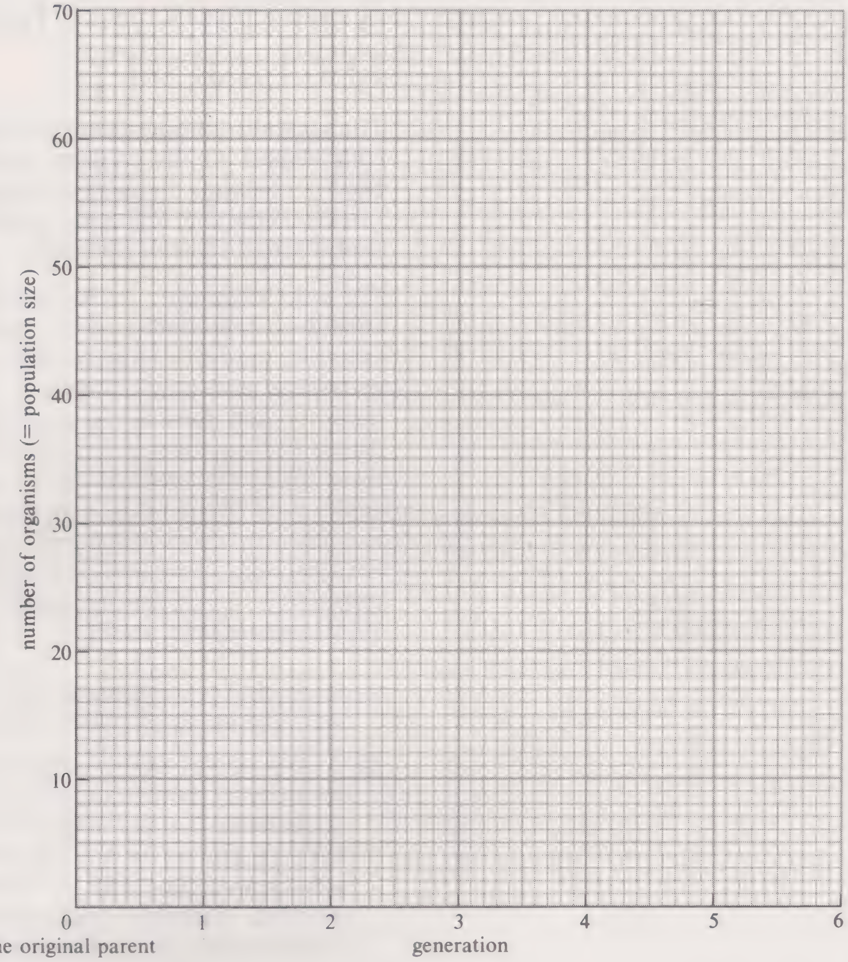


FIGURE 6 Growth in numbers over successive generations (blank graph).

It is convenient to introduce a new term at this point. One often needs to refer to a group consisting of all organisms of the same kind (such as buttercups, or lions or people), living in the same area and capable of breeding with one another to produce offspring. Such a group is known as a **population**. The graph that you plotted on Figure 6 shows how a population grows over successive generations. You will learn more about the factors that affect population growth in Unit 25.

Populations cannot continue to grow at ever increasing rates for more than a few generations, because they would soon run out of food, water and space in which to live. Moreover, predators and disease also limit population growth. It is more usual to find that population numbers remain either fairly stable, or oscillate around some average value (we shall discuss the reasons for this in Unit 25). Because of this, only a fraction of an organism's reproductive potential is realized. Many of the eggs it lays or the seeds it produces never themselves develop to maturity; that is, an organism's *actual* fitness usually falls far short of its *potential* fitness.

Consider the factors that affect an individual's fitness. Imagine that there exist two distinct phenotypes of a particular kind of plant, one with prickles and one without. Refer to Table 4, which shows how these two kinds of plants fare when growing in clumps side by side in identical conditions of soil, illumination and water supply.

□ As the smooth plants produce more seeds than the prickly plants, is it reasonable to conclude that they are fitter than the smooth plants? If so why? If not, why not?

■ No, it is not reasonable to conclude this. As you saw in Section 4, the fitness of an organism is defined as its ability to leave offspring *that are themselves able to produce offspring.* Using this definition, prickly plants are fitter than smooth ones, because each of them leaves five offspring that produce seeds, whereas each smooth plant leaves only three.

TABLE 4 Survival of a clump of prickly plants and a clump of smooth plants

Prickly plants	Smooth plants (i.e. without prickles)
each plant produces 100 seeds	each plant produces 120 seeds
30 of these germinate and grow	30 of these germinate and grow
11 of these seedlings are eaten 12 are killed by drought 2 die through fungal attack	23 of these seedlings are eaten 2 are killed by drought 2 die through fungal attack
5 survive to maturity and produce seed	3 survive to maturity and produce seed

Notice from Table 4 that the factors that affect an individual's fitness can be divided into two broad categories; factors that directly affect the plant's reproductive capacity, and those that affect its ability to survive to maturity. First, one plant can differ from another in the number of seeds it produces. The plant that produces the greater number of seeds is said to be the more fecund. In general, the number of fertilized eggs which a sexually reproducing organism helps to produce is referred to as the organism's **fecundity**. Thus the smooth plants in Table 4 are more fecund than the prickly ones. Second, one plant can differ from another in the fertilized egg's chances of surviving through to reproductive maturity. The plant whose seeds survive better is said to have the greater **viability**.

An organism's fitness is therefore affected by at least two major components: its fecundity and its viability. It is important not to confuse these terms.

□ Bearing Table 4 in mind, decide which four factors in general will prevent an organism from surviving through to maturity.

■ (i) Failure of the fertilized egg to develop properly. (The processes that control normal development in the seed or in the embryo, may be faulty; development may come to a halt and/or the developing organism may die.)

(ii) Death through being eaten.

(iii) Death through starvation of resources.

(iv) Death through disease.

□ Is an organism that is more fecund than another necessarily more viable? (Refer to Table 4).

■ No. Table 4 shows that the smooth plants are more fecund than the prickly ones. However, only 3 out of 120 seeds of the smooth plants survive to maturity, that is 2.5%, whereas 5 out of 100, that is 5%, of the seeds of the prickly plants survive to maturity. Therefore the prickly plants are more viable.

Table 4 illustrates three further points about fitness:

1 The fitness of an organism has meaning only when defined with reference to a specific environment. If the environmental conditions change, then the fitnesses of different phenotypes will almost certainly change as well. For example, Table 4 shows that prickly plants are more susceptible to drought than smooth ones. Hence, if the fitnesses of the two phenotypes were compared in a wet rather than a dry environment, it is likely that far fewer prickly plants would die, and their fitness relative to smooth plants might be much greater.

2 Although viability and fecundity are numerical characteristics that can be experimentally measured for any organism, the concept of *fitness* implies a *comparison* between two organisms that differ in some clearly defined respect. In Table 4 the comparison is between smooth and prickly plants: for every three mature offspring of the smooth plants there are five of the prickly plants, that is, the smooth plants are 60% as fit as the prickly ones. This illustrates that fitness is a *relative* property, a point to which we return in Section 6.

3 The example quoted in Table 4 is hypothetical, and by its very simplicity might give the impression that the fitness conferred by a character is easy to measure. This is not so. Under natural conditions it would be extremely difficult to keep track of the fate of all of the plants, all of their seeds and the seedlings that grew from them. The difficulties would be just as great with many kinds of animal. Also, it would be wrong to assume that the difference in fitness between the prickly and the smooth plants was necessarily a direct consequence of their smoothness or prickliness.

□ Is there any evidence from Table 4 that the difference in fitness might not be the result of the presence or absence of prickles?

■ Prickles certainly seem to confer some degree of protection against predators because 11 out of 30 prickly plants were eaten compared with 23 out of 30 smooth ones. However, the smooth plants seemed to be able to withstand drought better, and it is hard to see how this could have much to do with the presence or absence of prickles. It is quite possible that smooth and prickly plants differ in other characters as well, and that it is these characters that affect their susceptibility to drought.

It is possible, therefore, to attribute differences in fitness directly to the presence or absence of a particular character only if the organisms being compared are identical in all other respects. Unfortunately, organisms do not differ from each other in this convenient way. If two organisms differ in one character, they almost invariably differ in many other characters as well.

SUMMARY OF SECTION 5

1 If unchecked, a population will grow increasingly rapidly as the generations pass.

2 Population growth rarely continues unchecked for long because there are not usually the resources available, and also because of predation and disease.

3 The differences in fitness of individuals in a population arise from two contributing components: viability and fecundity. Phenotypes of an organism with higher viability do not necessarily have higher fecundity.

4 Fitness is a relative term, the fitness of one phenotype being compared with the fitness of another. Fitness values only apply to the environmental conditions in which they are measured; a change in these conditions can lead to a change in the fitness values. In practice, fitness values are very difficult to measure.

SAQ 7 Which are more fecund, cod or humans? Give reasons for your answer.

SAQ 8 Which are more viable, cod or humans? Give reasons for your answer.

SAQ 9 Is a woodland a population of organisms?

SAQ 10 Using appropriate axes, sketch three graphs showing how many organisms would be present in five successive generations (0–4) of a population under each of the conditions (a)–(c). Assume that the organism dies the instant it gives birth. Assume also that there is one organism present in generation 0, that an organism can give birth without having to mate with another one, and that all organisms give birth.

(a) Each organism gives birth to one other organism in its lifetime.

(b) Each organism gives birth to two other organisms in its lifetime.

(c) Each organism gives birth to three other organisms in its lifetime.

SAQ 11 How does the growth of the population differ in the three circumstances described in SAQ 10? Can you make any generalization about the growth of populations from the graphs you drew in answer to SAQ 10?

SAQs 12 and 13 take longer to answer than SAQs 10 and 11. You should skip them if you are short of time.

SAQ 12 Marmosets are small monkeys that live in South America. Draw a graph that shows the numbers of marmosets present in a population in successive 6-month periods over 4 years, making the following assumptions:

(a) At the beginning (time = zero) there are one adult male and one adult female marmoset.

(b) The male and female are put together and take some time to settle down: they produce their first pair of infants after one year.

(c) Every birth always produces two infants.

(d) After the first pair of infants, the adults thereafter give birth every 6 months for 10 years.

(e) When it is 1 year old, each marmoset leaves its family group and pairs with another marmoset of the same age from the population, and each pair produces its first pair of infants when they are 18 months old.

(f) All animals in the population live for longer than 4 years.

SAQ 13 The assumptions made in SAQ 12, although not strictly valid, are not very far from reality. Given that this example is more realistic than those in SAQ 10, would you say that the marmoset population shows the same tendency to grow with increasing rapidity as the generations pass?

SAQ 14 Suggest three main kinds of causes that might affect the viability of lettuce plants in a garden. From your general knowledge, give specific examples of each kind of cause where possible.

6 THE INHERITANCE OF CHARACTERS

This Section shows that if one phenotype is fitter than another, organisms with the fitter phenotype will tend to increase in numbers as the generations pass, and those with the less fit phenotype will tend to decrease—provided that one important condition is satisfied. This is that the phenotypic character must be passed down from parent to offspring, that is, it must be inherited.

The preceding discussion shows that some phenotypes are fitter than others. The following exercise shows why this is relevant to evolution. You are asked to work out how the numbers of two phenotypes of different fitness change in a population over successive generations. In fact, you are asked to do two sets of calculations, one assuming that the phenotypic characters of the offspring resemble those of their parents, and the other that they do not.

6.1 EXERCISE ON CHANGES IN A POPULATION (TV PROGRAMME)

A population of a particular kind of plant is growing in a field. The seeds germinate in the late summer, and the plants over-winter as small seedlings. In the following spring the seedlings continue to develop, they flower in the summer and produce seeds, and then die. The seeds germinate in the late summer, and the cycle continues.

INHERITED/HERITABLE CHARACTER

Two distinct phenotypes can be recognized in the population. Plants of one phenotype are better able to survive through the winter than plants of the other. The two phenotypes can be called 'resistant' and 'non-resistant', respectively.

A team of botanists carries out a research project on this population of plants and discovers the following points.

1 30% of resistant plants survive the winter on average, whereas only 10% of non-resistant plants do.

2 At other times of the year, the two phenotypes are equally viable; they are also equally fecund.

3 All plants that survive the winter produce flowers.

4 From each plant that flowers, five seedlings develop in the late summer and autumn.

The botanists begin their research in the autumn and monitor the progress of 100 resistant seedlings and 100 non-resistant seedlings.

ITQ 3 (a) First assume that half of the seedlings that develop from the seeds of any plants are resistant and half are non-resistant, *regardless of whether the parent plants are non-resistant or resistant* (see Figure 7). That is, assume that offspring do not inherit from their parent plants either the ability to resist the winter, or the lack of this ability.

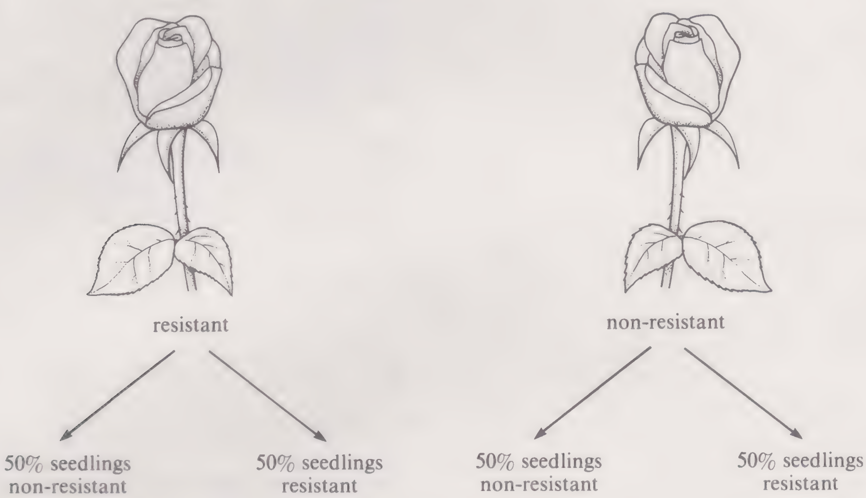


FIGURE 7 Resistance in parent and offspring plants.

Using this assumption, work out the numbers of resistant and non-resistant seedlings that would be expected in the population each autumn during the 3 years following the start of the experiment. Remember that in the first autumn, there are 100 resistant and 100 non-resistant seedlings in the field. Plot the results as a graph of numbers of seedlings present in each autumn against number of autumns after the start of the project. Your graph will have two lines, one for non-resistant seedlings and one for resistant seedlings. Use the blank graph in Figure 8a to plot your calculated values.

(b) Repeat the calculation, but this time assume that all of the seedlings that develop from resistant plants are themselves resistant, and all of the seedlings that develop from non-resistant plants are non-resistant. Again, remember that to begin with in the first autumn there are 100 resistant and 100 non-resistant seedlings in the field. Plot the numbers of resistant and non-resistant seedlings that would be expected each autumn during the 3 years following the start of the experiment. Use the blank graph in Figure 8b; again you will have two lines.

(c) Now compare the two graphs. What conclusions can you draw from them?

When you have completed this exercise look at the answers.

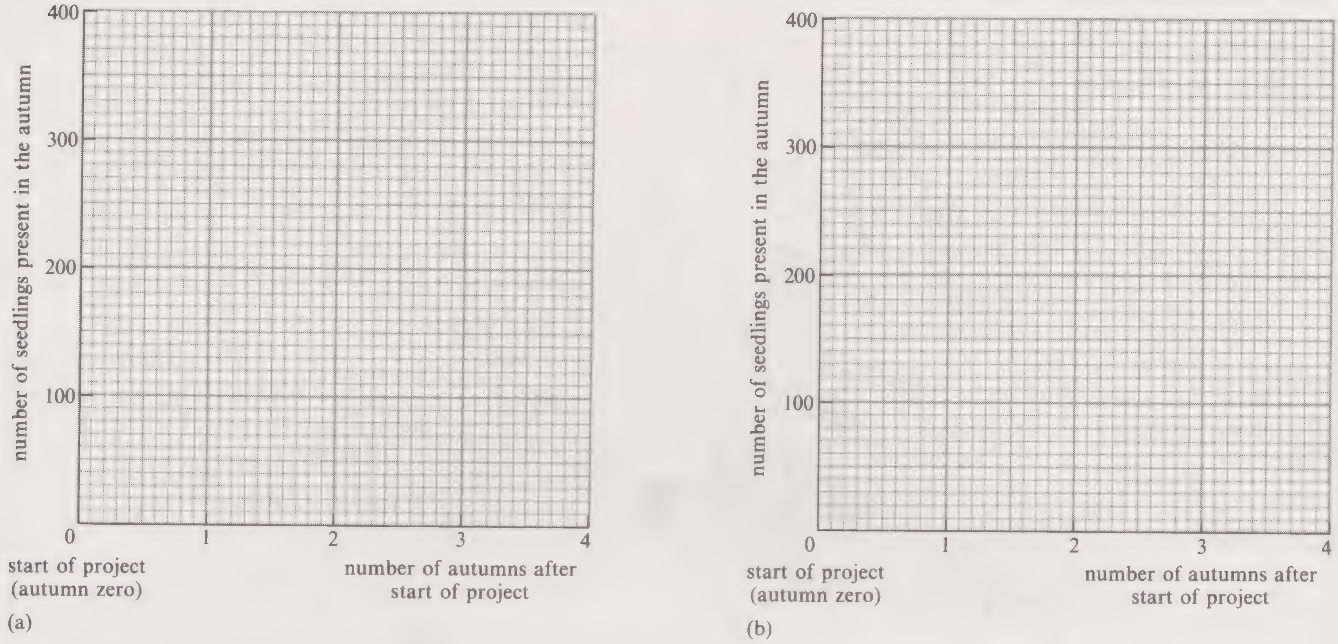


FIGURE 8 Number of resistant and non-resistant plants in successive years (a) assuming resistance is not inherited, and (b) assuming it is inherited (blank graph).

The exercise you have completed in ITQ 3 shows that if one phenotype is fitter than another, *and if the character is passed down from generation to generation*, then organisms possessing the favoured character will become more numerous and organisms possessing the character that confers less fitness will become less numerous as the generations pass. A character that is handed down from parent to offspring in this way is said to be an **inherited character**. The term **heritable character** is also used. If, however, a character is not inherited, but randomly acquired as the organisms mature, then, even though it may confer an advantage, its frequency will not change (except randomly) from generation to generation.

Are all the arguments produced so far in this Section just so much theory, or do they have any relevance to real life? How, indeed, are the results of this exercise relevant to the theory of evolution? Let us seek an answer by returning to the peppered moth. Enthusiastic naturalists have collected butterflies and moths in Britain for a very long time. It is known that in the early part of the 19th century, when the industrial revolution was only just getting under way, only the typical pale forms of the peppered moth were caught. The *carbonaria* form was first caught in Manchester about 1850, and from then on it became increasingly abundant, particularly in northern industrial areas; the typical form has become increasingly rare in those areas. In fact, in many industrial areas virtually all of the moths are *carbonaria*. The other dark-coloured form of the moth, *insularia*, has also become more abundant over the years. Figure 9 shows how the proportion of typical, *carbonaria* and *insularia* forms varied in the 1950s from one part of Britain to another. You can see that in Cornwall and the highlands of Scotland all the moths recorded are typicals, whereas in the North and Midlands, it is the *carbonaria* and *insularia* forms that predominate.

Note Figure 9 is overleaf.

Since the middle of the 19th century, therefore, in the industrial areas there has been a spread of the *carbonaria* and *insularia* forms at the expense of the typical form; this is because in those areas the *carbonaria* form is fitter. To complete the story, it only remains to mention that the typical, *carbonaria* and *insularia* characters of the moth are indeed inherited. This example shows very nicely, therefore, that given the conditions stipulated earlier, a population does indeed change its characteristics.

Clearly, then, the *carbonaria* phenotype is an adaptation to industrial environments—dark-coloured trees, to be specific. The adaptation is heritable and evolution has occurred. But evolution does not stop if there are still further alterations in the environment. Are there any reasons that might lead you to expect the number of the *carbonaria* forms to have fallen in industrial areas over recent years?

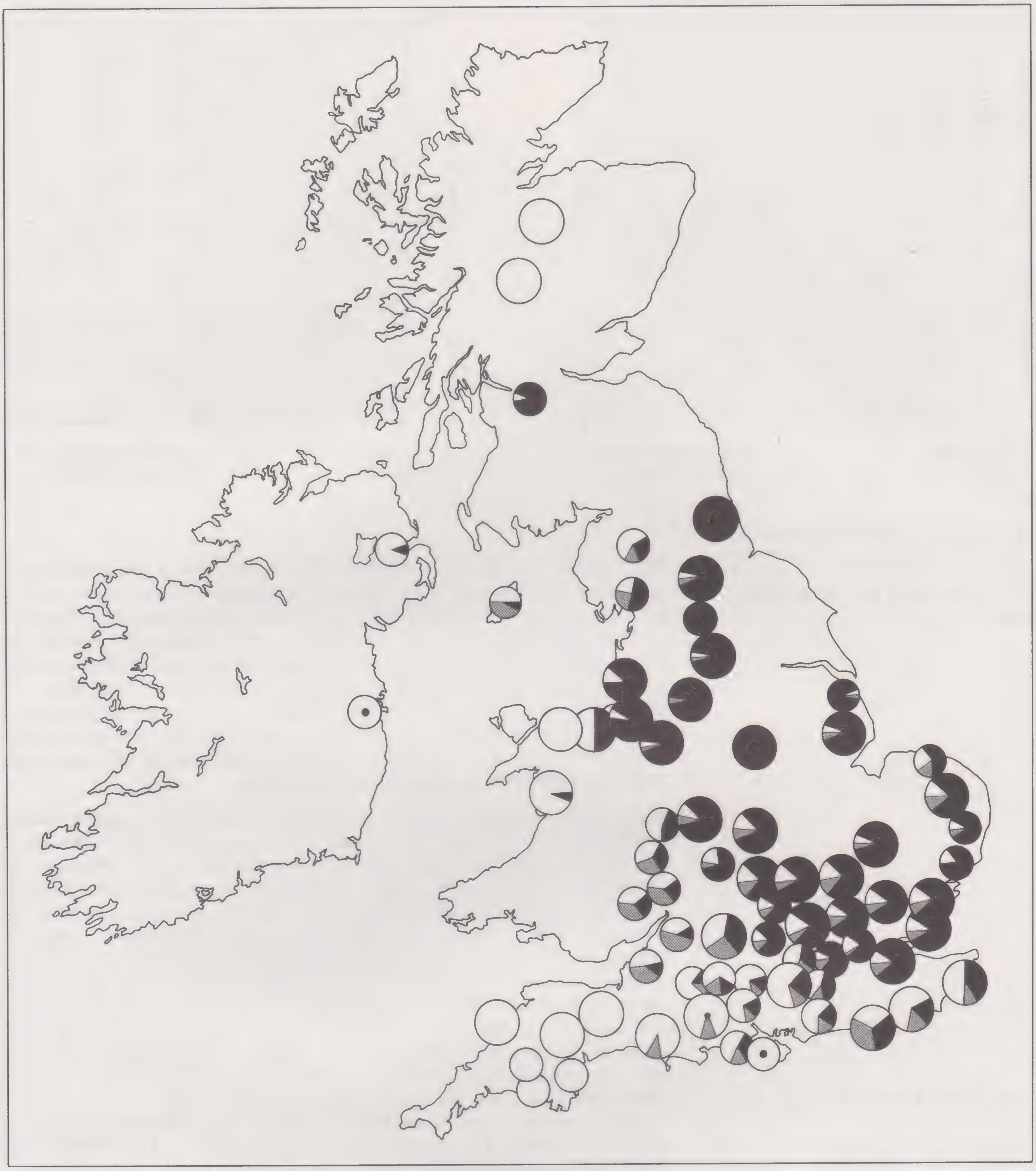


FIGURE 9 The relative frequencies of the three different forms of the peppered moth, *Biston betularia*, in different parts of Britain during the 1950s. The circles show the localities in which collections were made and the size of the circle indicates the number of moths in the sample. The size of the black area of each circle gives the percentage of *carbonaria*, the grey area the percentage of *insularia* and the white area the percentage of the typical form. A single dot in the centre of the circle means that only one moth of that variety was taken in the collection.

NATURAL SELECTION

With the passing of the Clean Air Act in 1958, the concentration of the two main air pollutants, soot and sulphur dioxide, has fallen. Figure 10 shows how sulphur dioxide concentrations in the air (expressed in $\mu g\, m^{-3}$) changed from 1960 to 1983 in the north-west of England and North Wales. The data came from a study by three biologists who have collected information on the peppered moth for some 25 years. Less soot in the air means lighter-coloured vegetation, and hence less camouflage for the *carbonaria* form. Less sulphur dioxide should also mean more lichen growing on tree trunks and walls, and hence greater camouflage for the typical forms. One should expect that these changes in camouflage should have an effect on the relative proportions of typical and *carbonaria* forms—and the expectation has been confirmed by experiment. The proportion of *carbonaria* forms collected in light traps and assembler traps has fallen at many sites in Merseyside and North Wales since the mid-1970s. So, comparatively recent environmental changes—through an effect on the relative fitnesses of the two forms—have brought about a change in their relative abundance that is, in effect, the reverse of what occurred in the 19th century. Thus we can see that, first one way at the time of the industrial revolution and the other way more recently, the nature of the environment has determined the relative fitnesses of the two forms. This process, the driving force of evolution, is termed **natural selection**.

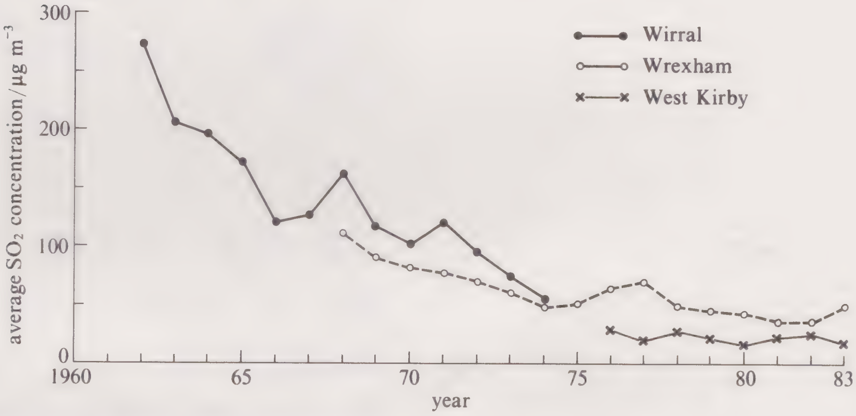


FIGURE 10 Changes in sulphur dioxide concentrations in the air ($\mu g\, m^{-3}$) from collecting sites in north-west England and North Wales.

The TV programme for this Unit describes something of the historical context in which the theory of natural selection emerged. It tells how the germ of the theory came to Darwin when, as a young man, he travelled round the world as ship's naturalist on H.M.S. Beagle, how the idea developed and matured over a 17-year period after Darwin's return to England, and how our view of the living world has been transformed by one of the great ideas of science.

Darwin rightly saw that inheritance was crucial to the theory of natural selection, and he made determined efforts to find out how the mechanisms of inheritance actually worked. The programme mentions some of the breeding experiments that Darwin carried out on plants and on pigeons. Darwin was unsuccessful in his efforts, but where he failed, another great 19th-century biologist, Gregor Mendel, succeeded. Unit 20 describes Mendel's work in more detail, and by pointing forward to this work, the TV programme provides a bridge between the two Units.

MUTATION

MUTANT

SUMMARY OF SECTION 6

1 This Section demonstrates that a necessary condition for evolution to occur is that the characters that evolve are heritable.

2 The typical, *carbonaria* and *insularia* colour characters of the peppered moth are inherited; this inheritance is a prerequisite for the known changes in the relative frequencies of the different colour forms to have been the result of natural selection.

3 The TV programme for this Unit describes something of the historical context in which the theory of natural selection occurred.

SAQ 15 From your general knowledge, which of the following characters do you think are inherited?

(a) Speaking the English language

(b) The blood groups to which people belong

(c) The rough hands of a manual worker

(d) The colour pattern of a tabby cat's fur

SAQ 16 Suppose that people were found to be fitter (in the sense described in Section 5, rather than in the sense of being physically fitter) when they had rough hands than when they had smooth. Bearing in mind the answer to SAQ 15, would you expect the frequency of rough-handed people to rise in the population over several generations? If so, why? If not, why not?

7 EVOLUTION BY NATURAL SELECTION: MUTATION AND MODELS

This Section shows that if the heritable characters of an organism's phenotype were able to change from time to time, and if there were also from time to time changes in an organism's environment that affected its fitness then one would expect the phenotypes of individuals within a population to continue to change as the generations passed. In short, one would expect the phenotypes of the organisms within the population to *evolve*. The Section then summarizes the theory of evolution by natural selection, and develops some evolutionary models.

7.1 MUTATION

The example of the peppered moth may seem rather trivial. All that has been shown is that if the environment becomes dirty when once it was clean, then *carbonaria* moths flourish and typical moths dwindle in numbers, and that if the environment becomes clean again, the reverse happens. It might seem from this that there is not much scope for change in Britain's peppered moth population other than this seesawing of the frequencies of the two colour forms as the environment changes. It might also seem that if any organism were chosen whose phenotypic variations are heritable and affect differently the organism's fitness, then all that one could expect is that the relative frequencies of those phenotypes would fluctuate in the population with changes in the environment.

One additional factor, however, changes a trivial phenomenon into an important one. This is that *new* heritable characters can appear in a population of organisms. A change in a heritable character is called a **mutation** and an organism that possesses a mutation is called a **mutant**. Note particularly that a mutation is heritable. Suppose, for example, that in a popu-

lation of normal buttercups growing in a field, a single plant with shrivelled leaves was found. If the shrivelled condition were due to an attack by a fungus, or to lack of water, then such a condition is not the result of a mutation and would not be heritable: the leaves of plants that grew from any of the buttercup's seeds would, in normal conditions, grow quite normally. If the shrivelled leaves were the result of a mutation, however, then the condition would be heritable, and the plants germinating from the seeds of the buttercup with the shrivelled leaves would inherit from the buttercup whatever it was that caused the leaves to be shrivelled.

Although individual mutations appear at random, there are some fairly regular features when the population as a whole is considered. In many organisms that have been investigated, all sorts of different mutant characters are found, but each of these tends to occur as a fairly well-defined proportion of the total population. For example, in humans, the disease called haemophilia, which is a condition in which blood clotting is impaired, is the result of a mutation that arises in 20 to 30 out of every million individuals. A mutant form of maize has shrunken rather than the normal seeds, and this mutation occurs on average once in every million individuals. Another mutant form of maize has an abnormal colour, and this occurs on average once in every 100 000 individuals. These figures may seem rather low; but if you remember that a population of organisms may well contain thousands of millions of individuals, then it is easy to see that mutant forms will occur quite frequently over a number of generations.

The reason that mutations are so important is that they provide a continual source of new phenotypes. To illustrate this, consider again the example of the peppered moth. Imagine that you are living at the beginning of the 19th century, and that the countryside is clean. Suppose that you have brought with you from the 20th century 100 typical and 100 *carbonaria* moths, and that you release these. You would not be surprised to find that all of the *carbonaria* were quickly eaten, and that only typicals survived. You would also not be surprised to find that the only peppered moths flying in the early 19th century were typicals. If there were no mutations, then there would be no *carbonaria* living at the beginning of the industrial revolution, and so none to benefit from the dirtier environment it brought about.

If, however, mutations occasionally occur, so that some moths descended from typical parents are *carbonaria*, then there would always be a few *carbonaria* moths in the population. There would, therefore, be a few living at the time of the industrial revolution, and these would be able to benefit from the changed environment. In fact, *carbonaria* have probably existed, in very small numbers, for as many million years as there have been peppered moths. They existed entirely *independently* of the industrial revolution. Mutations led to their brief appearance, birds ate them, their numbers diminished, renewed mutation gave a few more, and so on. Only when the environment changed and trees became dark did the mutation come into its own—and the relative fitnesses of the *carbonaria* and typical forms were reversed. (There is rather more to the story than is set out here, but these details—involving the relative fitnesses of the *caterpillars* of the two forms—are omitted.)

It is now known that mutation is not confined to one or two characters of an organism, but that many characters can be affected. Most mutants tend to be very unfit and leave few (if any) offspring. Despite this, the fact that the mutations occur means that there is in a population an enormous potential for variability. Should the environmental conditions change in such a way that a mutant that was previously less fit now becomes fitter than other organisms in the population, then gradually, as the generations pass, the mutant forms will increase in numbers, and the characteristics of the population will change. If the environment changes again, then perhaps another previously less fit mutant form will become fitter than others, and so will spread in the population, changing it even further. With all these mutant forms being produced, one would expect that over a sufficient number of generations, the phenotypes of the organisms would *evolve*.

COMPETITION

7.2 EVOLUTION REVIEWED

Mutation is, then, the final concept that is needed to formulate the complete theory of evolution by natural selection. The arguments that have been developed in Sections 3 to 7 can be summarized as follows:

1 The phenotype of an organism affects its fitness.

2 Individuals in a population differ in their morphology; some phenotypes are fitter than others. Differences in their fecundity, viability or both determine the overall difference in fitness.

3 Only a small proportion of the offspring produced by a parent generation in a population survive to maturity and reproduce. The most common causes of mortality of the offspring are lack of vital resources, predation and disease.

4 If the different characters that confer different levels of fitness are inherited, individuals with the fitter phenotypes will spread through the population at the expense of individuals that are less fit.

5 Because mutations occur, there are present in any population individuals that, under the prevailing environmental conditions, might not be as fit as other members of the population, but that might become fitter than other members if the environmental conditions were to change. This provides a huge potential for change, and allows the characters of populations of organisms to evolve over long periods of time.

This summary is, in fact, a statement of the theory of evolution by natural selection. The theory was first put forward in two papers read to the Linnean Society in London and published simultaneously in 1858 by Charles Darwin and Alfred Russel Wallace; it was developed more fully a year later in Darwin's book *The Origin of Species*. The main ingredients of Darwin's and Wallace's argument were the same as those listed above, although they did not develop their ideas in quite the same order as they are presented in this Unit. Briefly, they said that organisms produce more offspring than can survive; that there is, as a result, **competition** between them; that organisms show heritable variation; and that the fitter organisms survive at the expense of the less fit. To use their terminology, they said that organisms with characters that increased fitness were *selected for*, and so increased in numbers as the generations passed, and that organisms with characters that decreased fitness were *selected against*. They called the operation of factors such as starvation and disease, which rooted out the less fit individuals and favoured the fitter ones, *natural selection*. As a consequence, the full title of their theory is the theory of evolution by natural selection.

7.3 MODELLING EVOLUTION

The theory of natural selection provides an explanation of the mechanism by which evolution occurs. Like all theories, it is important to explore its implications. One way of doing this is to take something central to the theory, such as the concept of fitness, and see what quantitative predictions it is possible to produce by attaching actual fitness values to competing organisms. For example, if a population of a given plant contains two phenotypes, how rapidly will the proportion of the two phenotypes change over the generations if one phenotype is, say, one-half or one-tenth as fit as the other? What would happen to their number over the generations if the two were almost of equal fitness? Does there have to be a minimum difference between their fitnesses for the proportions of the two phenotypes to change?

It is clearly impossible to do experiments with plants of the requisite relative fitnesses to answer these questions because, as we mentioned in Section 4, it is extremely difficult to measure the relative fitnesses of differ-

ent phenotypes, let alone choose in advance plants of known relative fitnesses. Instead, one has to work out what one would expect to happen to the numbers of the two phenotypes, given certain assumptions to simplify the calculations. As you know from the earlier Units of this Course, it is often useful to construct a simple theoretical model to mimic a complicated real life situation, and then to investigate how the predictions of the model compare with reality. Modelling plays a large part in modern evolutionary theory, just as it does in other areas of science. Here we consider a simple model to examine what would be expected to happen to competing phenotypes with varying levels of relative fitnesses.

Consider a population of plants that contains equal numbers of two phenotypes: for example, a million of phenotype A and a million of phenotype B. The aim is to investigate how the numbers of the two phenotypes will change over the generations if phenotype B is 99% as fit as A; that is, if for every 100 offspring surviving to reproductive maturity that A produces, B produces only 99. To be able to answer this question we have to make a number of assumptions. In this model, the assumptions are designed to make the calculations as simple as possible. They are:

(i) There are no further mutations.

(ii) A plants always produce offspring of type A, and B plants always produce offspring of type B.

(iii) The number of A plants remains constant at one million over successive generations.

These simplifications are not totally unrealistic. One could imagine a situation in which A was holding its own over the generations, regardless of what happened to B, that B were marginally less successful, and that both tended to give rise to offspring that resembled their parents. With such a slight difference in fitness between A and B, one might doubt whether the relative numbers of A and B could change substantially over the generations, but is this doubt justified?

□ If there are a million individuals of each phenotype to start with, how many would there be in the first generation of offspring (offspring generation 1)?

■ There would be one million of phenotype A (assumption (iii)) and 99% of one million, or $10^6 \times 0.99$, which is 990 000 of phenotype B.

□ How many plants of phenotype B would there be in offspring generation 2?

■ There are 990 000 B plants in offspring generation 1. If these had been A plants they would have left an equal number of descendants, 990 000, in generation 2. However, B plants are 99% as fit as A plants, so they leave 99% of 990 000. And this (remembering that 990 000 is $10^6 \times 0.99$) is clearly $10^6 \times 0.99 \times 0.99$, which equals 980 100. You could go on and calculate the number of B plants in offspring generation 3 as 99% of 980 100, or $10^6 \times 0.99 \times 0.99 \times 0.99 = 10^6 \times 0.99^3$; the number of B plants in generation 4 as $10^6 \times 0.99^4$; and so on. In general, the number of B plants in offspring generation n would be $10^6 \times 0.99^n$, as you can see in Table 5.

TABLE 5 The number of B plants in successive generations in which the fitness of B plants relative to A plants is 99%

Generation	Number of B plants	
0	10^6	$= 10^6$
1	$10^6 \times 0.99$	$= 10^6 \times 0.99$
2	$10^6 \times 0.99 \times 0.99$	$= 10^6 \times 0.99^2$
3	$10^6 \times 0.99 \times 0.99 \times 0.99$	$= 10^6 \times 0.99^3$
⋮	⋮	⋮
n	$10^6 \times 0.99 \times 0.99 \times \cdots \times 0.99$	$= 10^6 \times 0.99^n$

Note: Generation 0 is the starting generation; generations 1 to n are the offspring generations.

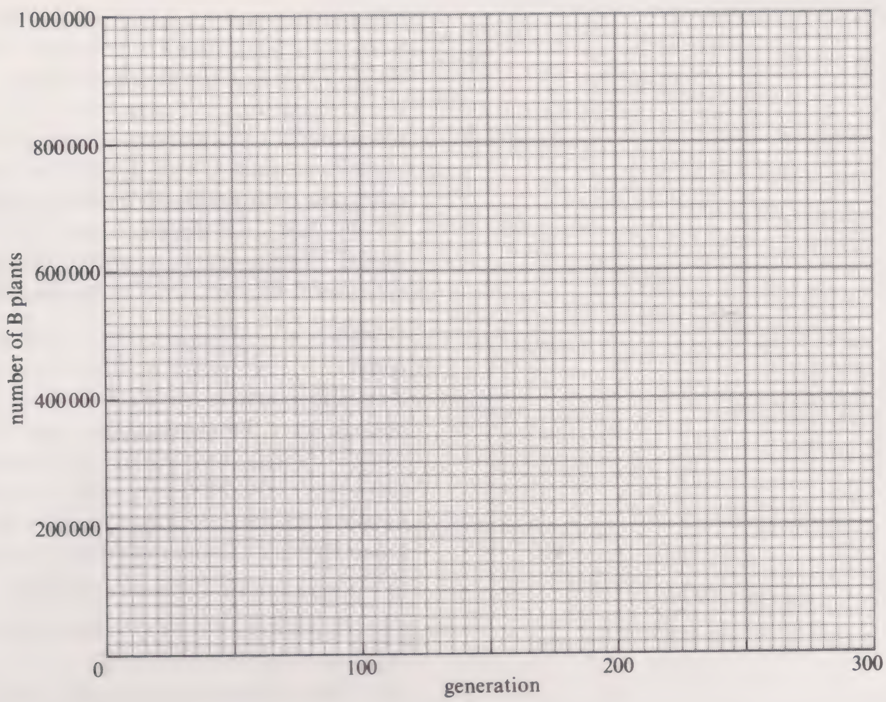


FIGURE 11 The number of B plants in successive generations when the fitness of B plants relative to A plants is 99% (blank graph).

ITQ 4 (a) Using your calculator, you should now complete the graph in Figure 11 to show the number of B plants that would be expected in generations 10, 50, 100, 150, 200 and 300.
(b) By generation 300, what percentage of the population consists of B plants?

ITQ 4 shows that even with a difference in fitness between two phenotypes as small as 1%, the proportion of the less fit phenotype would fall to less than 5% of the population in as few as 300 generations. Even if the plants only produced one generation per year, this change would be accomplished in 300 years, which, bearing in mind the 4 000 million years that have elapsed since life appeared on Earth, is no time at all.

What happens to the rate at which the numbers of B decline, if the relative fitness of B is changed? Suppose, for example, that B is 50% as fit as A, but that all of the other assumptions are unchanged.

□ After how many generations of offspring will B constitute less than 5% of the population?

■ The first generation of offspring will contain one million A plants, and 50% of one million, or $10^6 \times 0.5$, B plants. The second generation will contain $10^6 \times 0.5^2$ B plants, the third generation, $10^6 \times 0.5^3$, the fourth generation $10^6 \times 0.5^4$, and the fifth generation $10^6 \times 0.5^5$ B plants. The value of 0.5^5 turns out to be 0.031 25. Hence the fifth generation will contain $10^6 \times 0.031\,25$ B plants, which is less than 5% of the whole population of 1 031 250 plants (10^6 A + 312 50 B). So, *after only five generations*, the B plants would constitute less than 5% of the population. Clearly the greater difference in fitness between A and B has dramatically speeded up the rate at which B plants decline in the population.

From this kind of arithmetic, it is possible to derive a rule that relates the rate of decline of B to the difference in fitness between A and B under the set of assumptions that we are adopting in this model. The rule says that if the fitness of B relative to A is f (where f is a decimal number like 0.99), then the number of generations, n, required until B constitutes p per cent of the population is given by:

$$n = \frac{\log[p/(100 - p)]}{\log f}$$

The details of the equation are unimportant and you should not attempt to remember them. The important point is that, given a specific model, it is possible to make detailed quantitative predictions about the effects of fitness on changes in the proportions of the phenotypes in the population over the generations. What is more, once a model has been developed, it is possible to extend its use to answer a wide range of questions. For example, the model just developed shows that the number of B plants in the population will continue to diminish, generation by generation, until they virtually disappear. The model can also be used to explore the opposite situation of how a rare phenotype can spread in a population given the right circumstances. Work through the following exercise to show that this is so.

□ Consider a population containing two phenotypic forms of a plant. Plant X gives rise to offspring of type X, and plant Y to offspring of type Y. The number of X plants remains constant at 10^7 in each generation. In the starting population there are 100 Y plants, produced as a result of very low mutation rates from X to Y in previous generations. This mutation rate is so low that it can be ignored in the present calculations. There is a change in the climate with the result that Y, formerly slightly less fit than X, now becomes slightly fitter. Y's new fitness relative to X is 101%. Will the Y plants spread until they constitute at least 95% of the entire population?

■ The answer to this question requires only a slight modification of the model that we have developed. There are two stages to the answer. First, we need to calculate how many Y plants would be required to constitute 95% of the population. Second, we see whether it is possible to get a number as big as the calculated figure when Y's fitness relative to that of X is 101%.

Stage 1

We know that there are 10^7 X plants in the population in every generation. For the Y plants to constitute 95% of the entire population, there must be very large numbers of them indeed; many more than 10^7 X plants. We shall call this unknown large number m.

If there are 10^7 X plants and m Y plants in the population, then the *total* number of plants in the population will be $10^7 + m$.

If 95% of this total population are Y plants, we can write an equation:

$$\frac{\text{number of Y plants in population}}{\text{total number of plants in population}} = 0.95 \text{ (i.e. 95\%)}$$

We can now replace the words on the left-hand side of the equation with symbols.

$$\frac{m}{10^7 + m} = 0.95$$

We now have to rearrange this equation, to find the value of m.

Multiplying both sides of the equation by $10^7 + m$ gives:

$$m = 0.95\,(10^7 + m)$$

i.e. $m = 0.95 \times 10^7 + 0.95m$

Subtracting $0.95m$ from both sides of the equation gives:

$$0.05m = 0.95 \times 10^7$$

Therefore,

$$m = \frac{0.95 \times 10^7}{0.05} = 19 \times 10^7$$

This means that when there are 19×10^7 Y plants, they will form 95% of the population.

Stage 2

Discover whether it is possible for the number of Y plants in the population ever to rise to 19×10^7 or more, when Y's fitness relative to that of X is 101%.

Remember from the model that:

the first generation of offspring will contain 100×1.01 Y plants;

the second generation of offspring will contain 100×1.01^2 Y plants;

the *n*th generation of offspring will contain 100×1.01^n Y plants.

The simplest way to answer this question is to choose a large value for n, and calculate how big 100×1.01^n turns out to be.

Let n be 1 000.
Then,

$$\begin{aligned} 100 \times 1.01^n &= 100 \times 1.01^{1000} \\ &= 100 \times 20\,959 \\ &\approx 2.1 \times 10^6 \end{aligned}$$

This is smaller than 19×10^7, so we should try a bigger value for n.
Let n be 2 000
Then,

$$\begin{aligned} 100 \times 1.01^n &= 100 \times 1.01^{2000} \\ &= 100 \times 439\,286\,205 \\ &\approx 4.4 \times 10^{10} \end{aligned}$$

This is bigger than 19×10^7, so we have shown that after 2 000 generations, the Y plants will constitute well over 95% of the population.

This exercise demonstrates the important point that it takes only a slight shift in the relative fitnesses of two phenotypes in a population to bring about a total transformation in that population, with the result that a formerly rare phenotype can become the predominant form in the population. This means that even slight inherited differences in an organism's morphology, physiology, biochemistry, behaviour, or any other character that can affect its fitness can potentially have great evolutionary significance.

7.4 IMPLICATIONS OF THE THEORY OF NATURAL SELECTION

The theory of natural selection has been of great significance from the time that it was formulated through to the present day. Darwin's book, *The Origin of Species*, had, of course, immense impact upon the ecclesiastical world of Victorian Britain, which until that time was firmly wedded to a literal interpretation of the account given in the Old Testament about the beginning of life on Earth. To biologists, as well, the theory had very important consequences. It provided a consistent explanation of the mechanism behind evolution and so, if you like, made evolution respectable. This meant that biologists could now look at groups of organisms not in isolation from one another, but as related to each other in some way, just as a group of people with a remote common ancestor can work out how they are related.

Furthermore, and this comes back to the question of adaptation with which Section 3.1 opens, the theory made biologists very conscious of the importance of asking the question: 'How does this character affect the fitness of the organism?' It becomes a question that is important not just for the

individual organism concerned, but one that is relevant to the past and future evolution of the population of organisms to which the individual belongs. Contemporary biologists who study whole organisms, rather than their physiology or biochemistry, constantly ask questions such as: 'What is the advantage conferred by this structure, or by that bit of behaviour, or that character?' They ask about the *advantage* (or, to use an equivalent term, the *survival value*) because they believe that the features in question are adaptive, that they have helped the organisms possessing them to be fitter than those that lack them, and that they have therefore been selected for.

Although physiologists, biochemists and molecular biologists are less prone to ask questions about the survival value of the systems they are studying, implicit to much of their work is the assumption that those systems function efficiently. The theory of natural selection explains why it is important that they are efficient.

A final point is that two of the most fundamental characteristics of all living organisms, reproduction and replication, are central to the theory of natural selection. The theory is about the fate of an organism's descendants; about how well one organism's reproductive effort fares in competition with the reproductive effort of other organisms. The theory is also about the particular phenotypic characters that influence the fate of an organism's descendants. How these characters are passed on from generation to generation, how they are *inherited*, is, as you have seen, crucial to the theory, and how they are inherited depends upon the process of reproduction. When Darwin and Wallace put forward their theory, they knew very little about the mechanisms controlling the inheritance of characters. Since the time of Darwin and Wallace, biologists have discovered a great deal about these mechanisms and have realized their significance both for the theory of natural selection and for the whole of biology. For this reason, the next Unit introduces you to the study of heredity.

SUMMARY OF SECTION 7

1 This Section explains the evolutionary significance of mutation, that is, heritable characters. Mutations producing new characters increase the amount of heritable variability within a population and greatly increase the potential for evolutionary change. Different phenotypes within a population (such as *insularia* and *carbonaria* peppered moths) presumably arose as a result of mutation.

2 A summary of Darwin's theory of evolution by natural selection is given.

3 Evolutionary models can be used to predict rates of changes in numbers of different phenotypes in a population. Even a simple model can show that very small differences in the relative fitness of two phenotypes can produce significant evolutionary changes.

4 A fuller understanding of the theory of natural selection requires an appreciation of the mechanisms of inheritance.

SAQ 17 Summarize the evolutionary importance of mutation as it affects X and Y plants in the exercise involving X and Y plants in Section 7.3.

SAQ 18 Starting with the assumptions made in the same exercise, with the single difference that Y's fitness relative to that of X after the change in climate is 105%, show that the proportion of Y plants in the population would be less than half after 200 generations of offspring, and more than half after 250 generations.

SAQ 19 List the five main arguments that, together, constitute Darwin's theory of evolution by natural selection.

OBJECTIVES FOR UNIT 19

After you have worked through this Unit, you should be able to:

1 Explain the meaning of, and use correctly, all the terms flagged in the text. (*SAQs 1–3, 7, 8, 9 and 15*)

2 Interpret data from investigations into the ability of different phenotypes to survive. (*ITQ 1, SAQs 4 and 5*)

3 Explain why an organism's ability to survive affects its fitness. (*SAQ 6*)

4 Plot on graph paper changes in numbers of organisms within a population from generation to generation, given information on birth rates and other relevant features of the organism's life history; and assess how changes in the assumptions about birth rates and other relevant features affect the changes in numbers of organisms within a population from generation to generation. (*ITQ 2, SAQs 10–13*)

5 List three factors that can affect an organism's viability. (*SAQ 14*)

6 Explain why characters must be heritable if the fitness they confer is to bring long-term changes in their frequency within a population. (*SAQ 16*).

7 Explain why mutations are important if evolution is to occur (*SAQ 17*)

8 Use simple evolutionary models to predict rates of changes in numbers of different phenotypes in a population. (*ITQs 3 and 4, SAQ 18*)

9 Summarize the main arguments of Darwin's theory of natural selection. (*SAQ 19*)

ITQ ANSWERS AND COMMENTS

ITQ 1 Table 6 summarizes the percentages that you should have calculated. They are given to the nearest whole number.

TABLE 6 Percentages of moths released that were recaptured

	Typical	*carbonaria*
Birmingham	25	53
Dorset	14	5

The Table shows that a larger percentage of inconspicuous than of conspicuous moths was recaptured, both in Dorset and near Birmingham. Provided that it can be assumed that a *carbonaria* moth is as likely to be recaptured as a typical moth, it is justifiable to conclude that these different percentages mean that fewer of the conspicuous moths have survived. As the answer to the previous question in the text shows, this assumption seems reasonable.

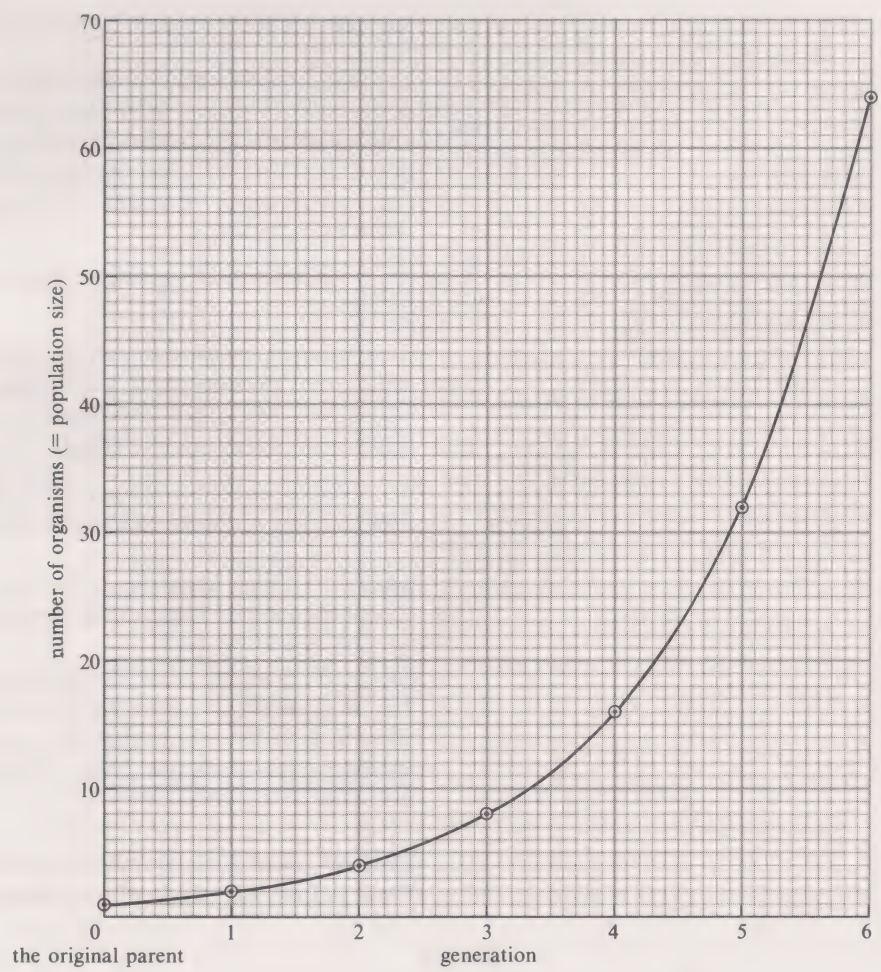
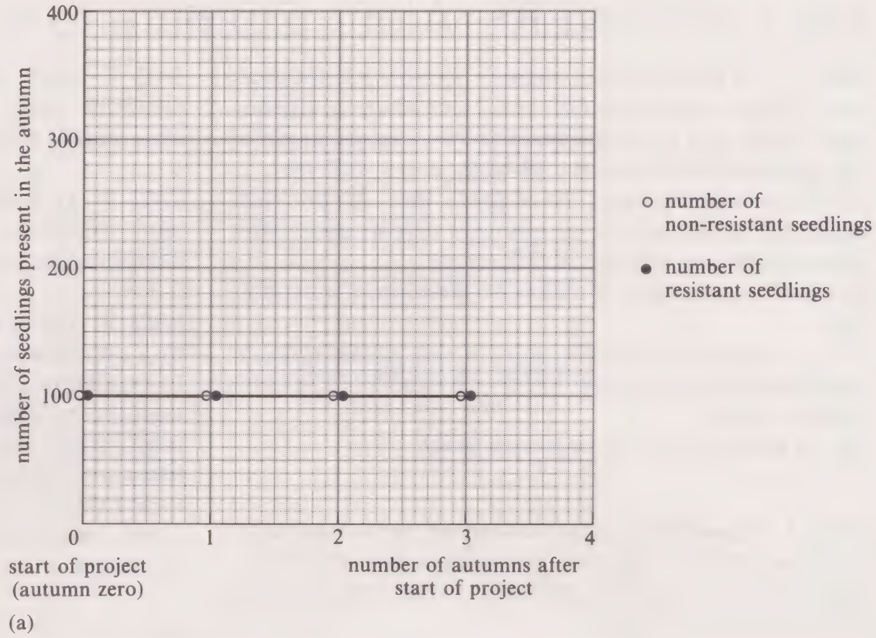


FIGURE 12 Growth in numbers over successive generations (completed graph for ITQ 2).

ITQ 2 (a) See Figure 12.

(b) Your graph should show that the number of organisms shoots up dramatically as the generations pass, and the rate at which it shoots up gets faster and faster. In the first generation there are 2^1 individuals, in the second generation 2^2, in the third generation 2^3 and in the xth generation 2^x. The rule that you need to use to calculate the numbers of organisms present in a particular generation, x, is to raise 2 to the power of x. The rule also works for generation 0 because $2^0 = 1$.

ITQ 3 Figures 13a and 13b show the plots you should have obtained. The obvious difference between Figures 13a and 13b (and 8a and 8b if you drew them correctly) is that the proportions of the two phenotypes in the population stay the same over successive generations in Figure 13a, but change in Figure 13b.



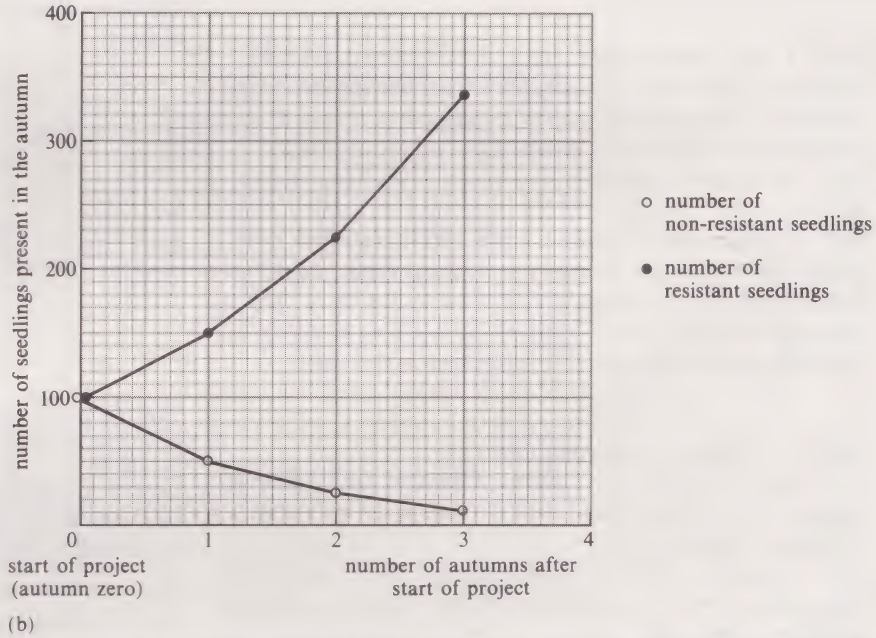


FIGURE 13 Number of resistant and non-resistant plants in successive years (a) assuming resistance is not inherited, and (b) assuming it is inherited (completed graph for ITQ 3).

ITQ 4 (a) Figure 14 shows what your completed graph should have looked like. If you got this wrong, look at Table 5. For example, the number of B plants in generation 50 would be $10^6 \times 0.99^{50} = 605\,006$.

(b) By generation 300 there are just over 49 000 B plants left. Together with the one million A plants this makes a total population of 1 049 000. Thus the percentage of B plants in the population is $(49\,000/1\,049\,000) \times 100 = 4.67\%$.

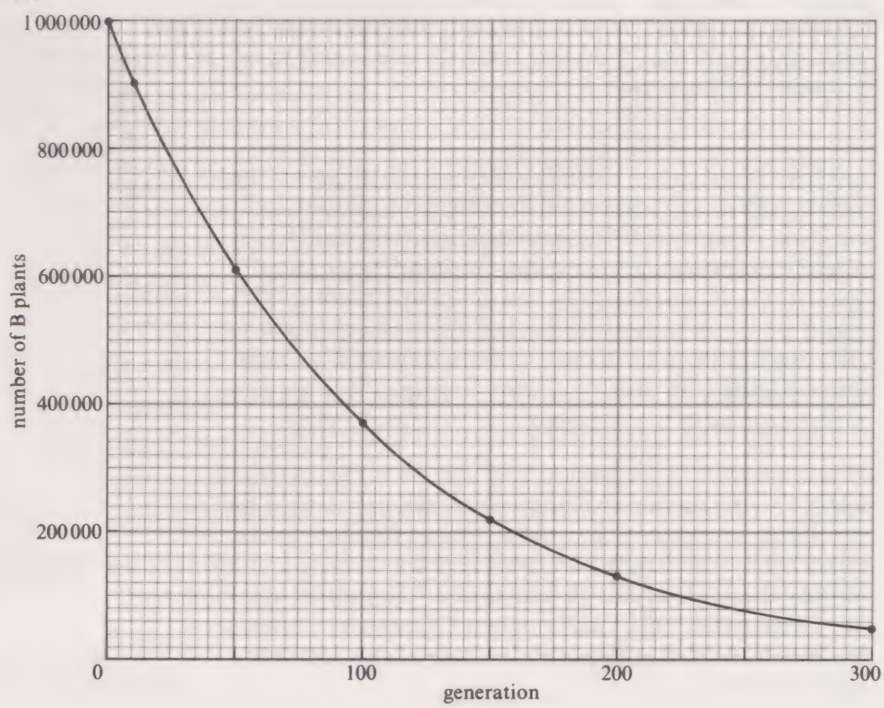


FIGURE 14 The number of B plants in successive generations when the fitness of B plants relative to A plants is 99% (completed graph for ITQ 4).

SAQ ANSWERS AND COMMENTS

SAQ 1 (e) is the correct answer. Section 3.1 discusses how certain mammals, fish and birds share a streamlined shape that is an adaptation to an aquatic mode of life, although their basic morphology is very different.

(a) is wrong because convergence has to do with superficial similarities in morphology despite underlying fundamental morphological differences.

(b) is wrong because it makes no mention of morphology.

(c) is wrong because the point about convergence is that the organisms should live similar kinds of lives, not different kinds.

(d) is wrong for the same reason as (c).

SAQ 2 A morphological feature of an organism is some aspect of its appearance or shape. (The word morphology comes from the Greek words meaning the study of form or shape.)

SAQ 3 (b) and (d) are correct answers because sound-sensitive organs and an escape routine that is performed whenever high-pitched pulses of sound are heard are both vital if moths are to escape from predatory bats.

(a) is unlikely to be adaptive because the bats do not hunt by sight.

(c) is debatable. If moths have well-developed eyes, and if these eyes can function well in the dark, then this feature may be an adaptation that helps moths to detect the approach of a bat. If the eyes do not function well in the dark, then they cannot be adaptive in this way.

SAQ 4 It must be assumed that:

(a) the ratio of the two colour forms in the captured sample truly reflects the ratio of these colour forms in the local population;

(b) a mouse's colour is of some significance in its life. If the mice live entirely underground, for example, it seems unlikely that their colour is at all significant. If, however, the mice live above ground and are eaten by predators who hunt by sight, then it is reasonable to suppose that the colour is adaptive.

SAQ 5 You could observe whether the mice in the two localities are indeed eaten by predators that hunt by sight. With careful experimentation, you could also directly observe whether predators eat different proportions of the colour forms in the different localities. You could also look to see whether the mice behave in a way that exposes them to the risk of being captured by predators hunting in this way (for example, by moving above ground in the daytime).

SAQ 6 Any animal that shows parental care would be a suitable example. If a mother looks after her young infant, then the chance that the infant will survive if the mother dies is likely to be less than if the mother lives on. Sometimes the male parent provides care—exclusively so, for example, in the case of the dotterel (a species of bird).

SAQ 7 Cod. Each mature male/female pair of cod produces many more fertilized eggs on average than each mature human male/female pair.

SAQ 8 Humans. Each human fertilized egg has a much higher probability of surviving through to reproductive maturity than does each cod fertilized egg.

SAQ 9 No. The definition says that all the organisms in a population have to be of the same kind, and have to be able to breed with one another. A woodland contains many different kinds of organisms, such as oak trees, dog's mercury, bluebells, rooks, earthworms, foxes, and so on. On the other hand, it is quite accurate to say that the oak trees in the wood constitute a population, as do each of the other groups of organisms just mentioned.

SAQ 10 (a) In this instance the population size remains unchanged from generation to generation (Figure 15).

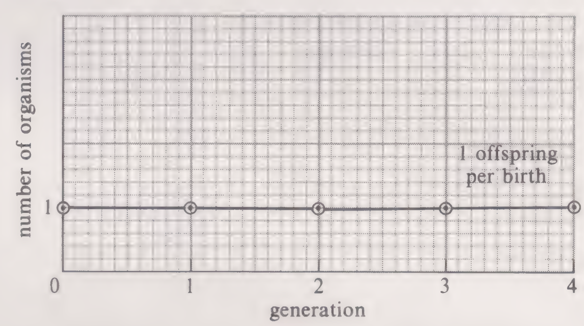


FIGURE 15 Numbers of organisms over successive generations (SAQ 10a).

(b) Your curve should look like the curve marked with the crosses in Figure 16. This case is identical to that described in ITQ 1.

(c) Your curve should look like the one marked by dots in Figure 16.

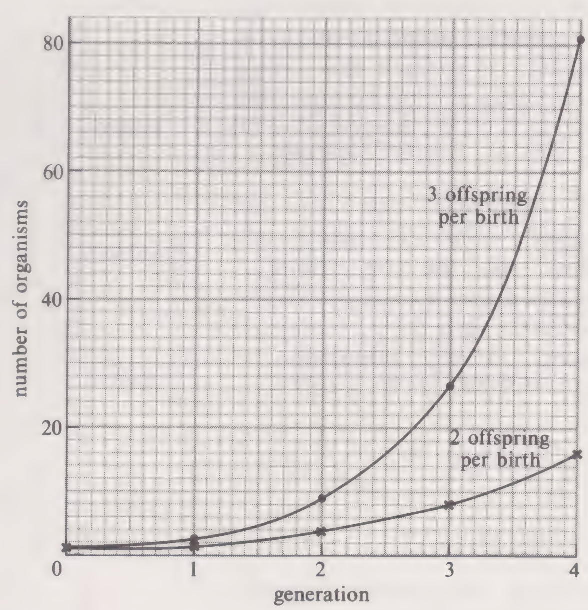


FIGURE 16 Numbers of organisms over successive generations (SAQ 10b and SAQ 10c).

SAQ 11 The population does not grow at all under the circumstances described in SAQ 10(a). The population size goes up increasingly rapidly with successive generations under the circumstances described in SAQ 10(b) and (c), but for (c) it goes up much more rapidly than for (b). Supposing that organisms actually exist that fulfil all the assumptions listed in SAQ 10, it would seem reasonable to make the following generalization: the more offspring an organism produces the faster the population will grow.

SAQ 12 You answer should look like the graph in Figure 17. If your graph does not rise as rapidly, you may have forgotten that once the animals born into the population are 18 months old, they too start to produce infants, further swelling the population size. Indeed, at 4 years from the beginning, the original pair's first grandchildren have started to produce infants.

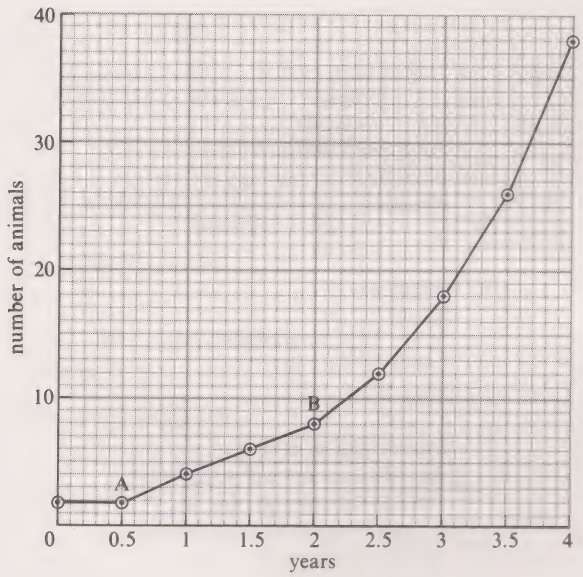


FIGURE 17 Numbers of organisms over successive generations (SAQ 12).

SAQ 13 In the first two years, the growth of the marmoset population is not very like the simple example given in SAQ 10. Thereafter, the two populations do grow in very similar ways. Figure 17 shows that the marmoset population does not grow at all in the first 6 months, and that the growth of the population follows a straight line from 6 months (A) to 2 years (B). From 2 years onwards, however, the marmoset population grows increasingly rapidly, just as in the simple example in SAQ 10.

SAQ 14 The lettuces might die through lack of resources, for example, insufficient water or light. They might be eaten by animals such as slugs. They might die from disease (for example, there is a fungus called *Rhizoctonia* that causes lettuce seedlings to collapse and rot).

SAQ 15 (b) and (d) are correct answers.

(a) The ability to speak a specific language such as English is not inherited. Children whose parents are able to speak English, if brought up in a household where, say, only French is spoken, will learn to speak French rather than English.

(b) Blood groups are inherited. If both parents belong to blood group O, for example, all their children will also belong to blood group O.

(c) The rough hands of a manual worker are not inherited. The roughness results from the manual work. The children of a manual worker will have soft hands unless they too take up manual work.

(d) The colour pattern of a tabby cat's fur is inherited. Mated pairs of tabby cats hand down the colour patterns of their fur from generation to generation.

SAQ 16 No, you should not. As hand roughness is not inherited, the children of rough-handed parents would have the same sorts of hands as the children of smooth-handed parents.

SAQ 17 If there had been no mutations from X to Y plants, there would have been no Y plants available in the population to take advantage of the change in climate that produced the changes in relative fitness values of the X and Y plants.

SAQ 18 If there are 10^7 X plants, then there will need to be 10^7 Y plants if they are to make up 50% of the whole population. After the change in climate, generation 1 will contain 100×1.05 Y plants, generation 2 will contain 100×1.05^2 Y plants and generation 200 will contain $100 \times 1.05^{200} = 100 \times 17\,293 \approx 1.7 \times 10^6$ Y plants. This value is *smaller than* 10^7, so after 200 generations the Y plants constitute *less than* half of the population.

In contrast, generation 250 will contain $100 \times 1.05^{250} = 100 \times 198\,301 \approx 1.98 \times 10^7$ Y plants. This is *larger than* 10^7, so after 250 generations the Y plants constitute *more than* half of the population.

SAQ 19 Refer back to Section 7.2 (p. 32) to check your answer. Note that you ought to be able to state from memory the five main points listed there. This does not mean that you have to memorize the exact wording used, but you should certainly be able to state the main ideas.

ACKNOWLEDGEMENTS

Grateful acknowledgement is made to the following for permission to reproduce Figures in this Unit:

Figure 1 Bodleian Library, Oxford; *Figure 2(a)* (*left*) Dr Peter Gould, Middlesex Hospital, London; *Figures 2(a)* (*right*) *and 2(c)* Kessel, R. G. and Kardon, R. H. *Tissues and Organs: a text-atlas of scanning electron microscopy*, copyright © 1979 W. H. Freeman and Company; *Figure 2(b)* Alberts, B. *et al. Molecular Biology of the Cell*, 1983, Garland Publishing Inc.; *Figure 2(d)* H. W. Woolhouse and G. J. Hills, John Innes Institute, Norwich; *Figure 4* Down House and the President and Council of the Royal College of Surgeons of England; *Figure 9* Sheppard, P. M. (1975) *Natural Selection and Heredity* (4th edn), Hutchinson; *Figure 10* Clark, C. A., Mani, G. S. and Wynne, G. (1985) Evolution in reverse: clean air and the peppered moth, *Biol. J. Linn. Soc.* **26** (2).

INDEX FOR UNIT 19

PLATE 1 A stick insect on a contrasting background.

PLATE 2 A stick insect on a background against which it is camouflaged.

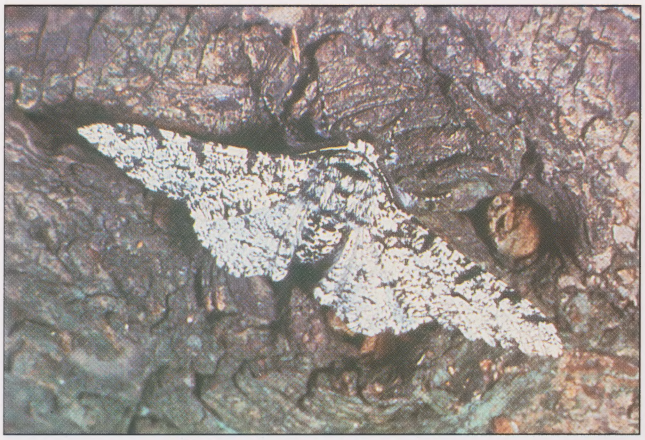


PLATE 3 The typical form of *Biston betularia*.

PLATE 4 The *carbonaria* form of *Biston betularia*.

PLATE 5 The *insularia* form of *Biston betularia*.

PLATE 6 Lichen on the bark of a tree.

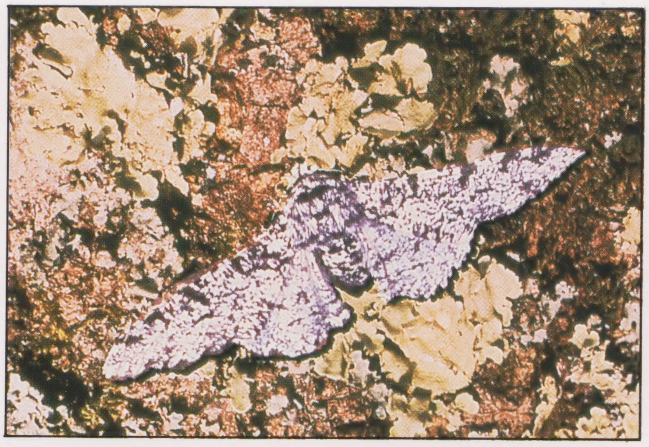


PLATE 7 The typical form of *Biston betularia* seen against the bark of a tree from a rural area.

PLATE 8 The *carbonaria* form of *Biston betularia* seen against the bark of a tree from a rural area.

PLATE 9 The typical form of *Biston betularia* seen against the bark of a tree from an industrialized area.

PLATE 10 The carbonaria form of *Biston betularia* seen against the bark of a tree from an industrialized area.